III. *On Apogamy and the Development of Sporangia upon Fern Prothalli.*

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[Plates 7–11.]

Introduction.

The two chief modifications of the normal course of the life-history of a fern, apogamy and apospory, are of interest in themselves, but have acquired a more extended importance from the possibility that their occurrence may aid in indicating the true relation between the sexual and spore-bearing generations, and so throw light on the nature of "alternation of generations" in archegoniate plants. This aspect has been recognised since the discovery of the phenomena, and will be best appreciated by tracing the progress of opinion on the nature of alternation from the time of Hofmeister to the present day. Only the more important contributions bearing on the subject can be mentioned in this place.

With the publication of the 'Vergleichende Untersuchungen' (1851), the fact of the regular alternation of a sexual with an asexual generation in the life-history of Bryophyta, Pteridophyta, and Gymnosperms was established. Hofmeister subsequently extended the observation to Angiosperms. In the work mentioned, and in the 'Higher Cryptogamia,' published some ten years later, no views as to the nature of alternation of generations are discussed. With the extension of accurate knowledge of the life-histories of Thallophytes, the attempt was made to compare the different individuals of the same species of Algæ and Fungi with the sexual and asexual generations of archegoniate plants. Two main views of the nature of alternation in the latter were put forward. On the one hand, Celakovsky* regarded alternation of generations in the Archegoniatæ and a few Thallophyta as essentially different from that found in the majority of the latter group. He distinguished the two types as antithetic and homologous alternation respectively. Pringsheim,†

* 'Sitz. d. Ges. d. Wiss. in Prag,' 1874, p. 21.

† 'Pringsh. Jahrb.,' vol. 11, 1877.

however, held that the sexual and spore-bearing generations were homologous with one another, alike in Thallophyta and Archegoniatæ. In support of this view he relied upon the instances of apospory which he had experimentally induced in Mosses,* together with the occurrence of apogamy in Ferns, the first case of which had been discovered by FARLOW† a few years before. He also compared the life-histories of a number of Thallophytes with one another and with that of the Moss, and showed how the reduction of the first neutral generation in some of the former led to a condition of things not dissimilar to the relation existing between the moss sporogonium and the sexual plant. Additional cases of apogamy in Ferns were subsequently discovered by DE BARY‡ and the subject fully discussed. Subsequently DRUERY§ found the first instance of an aposporous fern, and this and other examples were investigated by BOWER.||

It is unnecessary to go into further detail with regard to these deviations from the normal life-history, of which many additional instances have been recorded among Leptosporangiate Ferns.¶ Enough has been said to show the importance which may attach to a fuller knowledge of these phenomena in considering the nature of alternation. This subject has been discussed in recent years by BOWER,** VAIZEY,†† and STRASBURGER,‡‡ from the standpoint of the theory of antithetic alternation, and from that of homologous alternation by SCOTT.§§

In this paper the results of a series of cultures of fern prothalli will be described. They were commenced in the Jodrell Laboratory of the Royal Gardens, Kew, in 1895, and have been continued for two years and a-half. They have yielded examples of apogamy and related phenomena, the most striking being the production of sporangia upon the prothallus.|||| Since a connection can be traced between the occurrence of these abnormalities and the conditions under which the cultures were made, a short account of these will be given. After this the observations on the different species will be described in order, and in the following section treated comparatively. Finally, the bearing of these and other cases of apogamy on the nature of alternation of generations will be discussed.

* 'Monatsber. d. K. Akad. d. Wiss. Berlin,' 1876.

† 'Q. Jl. Micro. Sci.,' 1874, p. 266.

‡ 'Bot. Zeit.,' 1878, p. 499.

§ 'Linn. Journ.,' vol. 21, 1884, p. 354.

|| 'Trans. Linn. Soc.,' 1887, p. 301; also, 'Linn. Journal,' vol. 21.

¶ This is the most convenient place to note the fact that Mr. DRUERY, in referring to these phenomena, refers to "the possibility . . . for the prothallus to bear spores direct, and shut out the fern proper altogether," 'Choice British Ferns,' p. 40. This will be seen below to have been, in a sense, realised.

** 'Ann. Bot.,' 1890.

†† 'Ann. Bot.,' 1890.

‡‡ 'Ann. Bot.,' 1894.

§§ 'Brit. Assoc. Report,' 1896, p. 992.

|||| In a preliminary statement published in the 'Proc. Roy. Soc.,' 1896, p. 250, the two species which shared this peculiarity were briefly described.

REMARKS ON METHODS AND THE CONDITIONS OF CULTIVATION.

The cultures were carried out under similar conditions. It will be seen in a later section that an explanation of the agreement existing in the results for the different species is to be sought in this fact. The character and amount of deviation from the conditions which exist in nature are especially important for this purpose.

The spores were sown upon soil consisting of a mixture of vegetable mould and sand: this was thoroughly sterilised by first heating to 120° C. in a hot air steriliser, then to 100° C. in the steam steriliser after it had been placed in the flower pot, and finally, by moistening it with boiling water. After the pot, which was covered with a glass plate, had cooled, the spores were scattered over the surface of the soil, and the culture removed to the greenhouse attached to the laboratory. No fern plants bearing sporangia were growing in this house, and no sowings were made in it. The air was thus kept as free as possible from floating spores, and, to further guard against infection of the cultures, the glass plates were kept constantly on the pots. When the surface of the soil becomes closely covered with prothalli this danger is much lessened, and the necessary observations could be made more freely. Spores of fungi are always introduced along with the fern spores. They were readily kept in check, without injury to the young prothalli, by watering with a dilute solution of potassium permanganate.

The pots stood in saucers filled with water, or were surrounded with moist coco-fibre. Watering from above was avoided—this rendered fertilisation infrequent, and the prothalli continued to grow for a long period. This was, perhaps, the most important departure from natural conditions. It is further to be recognised that exposure to direct sunlight, and possibly the increased temperature, rendered the circumstances in which the prothalli grew very different from those under which we find them in nature. This difference would have been present in the case of shade loving organisms in any season, but was very marked during the summer of 1896. Dr. CHREE, the Superintendent of the Kew Observatory, has kindly supplied me with a record of the bright sunshine and the mean maximum temperature for the months of 1896, as compared with the average for the preceding nineteen years. From this it appears that in the months preceding August, 1896, the time at which sporangia were first observed on prothalli, both the percentage of possible hours of bright sunshine and the mean maximum temperature were in excess of corresponding averages for the preceding years. In the beginning of 1897 the cultures were removed to Glasgow, and grown in a fern case in a dwelling room. They were thus less exposed to bright sunshine.

The method described has been found to insure almost perfectly pure cultures. The results were in all cases checked by determining the characters which distinguished the prothalli and young plants of the different species from one another. The shape of the old prothalli, the presence or absence of glandular hairs upon them, and the

appearance of the ramenta and first leaves of the sporophyte were the most useful characters for this purpose.

Scolopendrium vulgare, L.

Considerable interest attaches to this species on account of the deviations from the normal life history cycle which occur in some of its numerous cultivated varieties. Apospory is recorded in two of them. In one* the prothalli arise from the margin of the leaves when portions of the latter are laid on damp soil, while in the other† the phenomenon is only exhibited by the first few leaves of the young plant which produce prothalli when still attached to the stem. I am not aware of any description of apogamy in *Scolopendrium vulgare*, though prothalli of peculiar form,‡ resembling some of those described below, have been briefly recorded by Mr. E. J. LOWE, F.R.S.

Spores of the varieties *ramulosissimum*, WOLL., and *marginale*, obtained from plants growing in the open air in the Royal Gardens, Kew, were sown in December, 1895. The prothalli of the two varieties were in many respects similar, and will be described together. Since, however, some peculiarities have only been observed in the case of the variety *ramulosissimum*, the description is based on the examination of its prothalli, except where the variety *marginale* is specially mentioned. Prothalli of ordinary form and texture developed from the spores; they bore sexual organs and upon some normal embryos arose. Many, however, owing to the conditions of cultivation remained unfertilised, and these continued to grow, while those on which the young plants were borne withered and died. The unfertilised prothalli soon lost the flattened form and the result of their further growth was in most cases a structure, which, on account of its form when typically developed, will be spoken of as a *cylindrical process*. Plate 7, fig. 1, represents a prothallus which has continued its growth in this manner. It is evident that in this case the cylindrical process has arisen from the apical region. This is its more common mode of origin in *Scolopendrium*, but in a small proportion of the prothalli it arose in a different position. The growth of the prothallus ceased and a cylindrical process, of similar form and structure to that shown in fig. 1, was developed from the under surface just behind the apex (fig. 2). Other prothalli grew on as a narrow thick structure which retained, however, the distinction between upper and lower surfaces; no sharp line could be drawn between this and a cylindrical process. The latter has lost the dorsiventrality of a normal prothallus. Archegonia, and sometimes antheridia, are present on all sides of it, but when rhizoids are abundant and well developed they are usually confined to the side turned to the soil. The structure of a cylindrical process is usually very simple; the tissue consists wholly of

* DRUERY. 'Journ. Linn. Soc.,' vol. 30, p. 281.

† LOWE. 'Journ. Linn. Soc.,' 1896, p. 529.

‡ 'Gardener's Chronicle,' Nov. 10, 1895.

parenchymatous cells, which towards the centre are slightly elongated, while the arrangement of the more superficial cells usually suggests the occurrence of periclinal divisions. Tracheides are absent in the majority of cases; their occurrence will be considered along with instances of apogamy. Fig. 3 represents the transverse section of a thin cylindrical process. The fact that a normal embryo was occasionally found on a process shows that the sexual organs are functional. Such a cylindrical process may continue to grow for a considerable time and attain a length of between one and two centims. Various modifications may, however, occur. These probably depend upon changes in the external conditions, although at present the connection can only be inferred. The process may reassume the form of a flattened prothallus with a distinct apical depression (fig. 4). This change appears to be favoured by a change of conditions in the direction of lower temperature, less direct illumination, and, perhaps, greater humidity of the atmosphere. Many prothalli exhibited it on their removal from the greenhouse at Kew to a fern case in Glasgow. Under the same circumstances, gametophytic budding from the surface of the process was frequent; the small prothalli usually bore antheridia only.

Apogamy occurred in connection with the cylindrical process. In the simplest case the apex of the process continued directly as the stem apex of the sporophyte. In the earliest stage recognisable by the naked eye (fig. 5) the tip of the process became yellowish, contrasting with the deep green colour of the region behind. Shortly after this, and before any indication of the first leaf, ramenta were developed. They were still very small in the specimen figured, but rapidly increase in size and number, and soon completely clothe the tip of the process. The boundary between the sporophyte and the process is usually clearly marked; archegonia occur to just behind the ramenta. The apogamously produced bud in fig. 8 is at this stage: its place of origin is, however, different, and will be referred to below. Soon after this the first leaf becomes recognisable from the outside, and a bud consisting of several leaves surrounding the stem apex is formed before any trace of a root is visible. The origin of the latter member has not been observed in the examples investigated. Sometimes, in addition to the bud arising as a continuation of the apex of the process, another may be produced laterally, or two buds of similar size may form side by side on the tip.

Returning to the earliest stage, fig. 6 represents part of a section in the direction of the dotted line in fig. 5, including the apex of the sporophyte. The most striking feature of the section is the definite though irregular line of demarcation between the cells of the process and the tissue of the sporophyte. The contrast depends mainly on the fact that the sporophyte tissue consists of small cells of meristematic appearance, while the cells of the prothallus have large vacuoles and thicker walls, which stain deeply with Bismarck brown. Occupying the apex an initial cell of the usual form is seen, and the succession of cell walls shows that segmentation proceeds as in the apex of a fern stem. In a central position and separated from the

sporophyte tissue, which it resembles in all respects, is a small group of cells. Other sections of the series showed that at one point this group was continuous with the main mass of sporophytic tissue, and that some of its cells had developed into tracheides. These were the only tracheides present at this stage. In fig. 7, which represents the longitudinal section of a similar bud at a slightly later stage, the corresponding tissue forms a considerable strand. This can be traced back in the axis of the process some distance behind the region to which the development of archegonia extends. The strand is here clearly seen to be continuous with the tissue of the young sporophyte. A comparison of these two stages of apogamous development in *Scolopendrium* leads to the view that the first change occurred in certain cells within the apex of the process. The latter then continued its growth as a sporophyte. Tracheides first appear in the tissue farthest from the apex. Subsequently, as examination of older specimens showed, tracheids are formed in the meristematic tissue beneath the insertions of the first leaves, and extend thence into the leaf stalk.

The origin of separate members of the sporophyte must be placed in connection with the apogamous development of normal buds. The resemblance between these phenomena and the occurrence of sporangia will be apparent; the latter will, however, be more conveniently considered separately.

Fig. 9 represents a prothallus, from the under side of which, near the anterior margin two new growths had started. That to the right was obviously a prothallus and bore a number of antheridia. The structure on the left was more complicated; at its insertion on the prothallus it was prothalloid, though no sexual organs were present. It continued, however, into a long narrow structure, the hairs on which resembled those found on young leaves; at one side near the base was a larger ramentum. The contrast between the tissue of the rudimentary leaf, with its air filled intercellular spaces, and that of the prothalloid expansion was sharply marked.

The instances of the growth of roots, unassociated with other members of the sporophyte, from a cylindrical process were more numerous. Fig. 10 shows an extreme example. From the massive branched process of this prothallus ten roots, one of which was of considerable length, arose; others still enclosed in the tissue of the process were found on cutting sections. Some of the roots had penetrated the soil, and doubtless aided in the nutrition of the large cylindrical process from which rhizoids were absent. The single long root seen in fig. 11 was borne on a prothallus of *Scolopendrium vulgare*, var. *marginale*. In this case numerous archegonia were present on the process close to the place of origin of the root.

The appearance of the tissues around the base of these roots pointed to their origin being endogenous, and the study of sections confirmed this. Thus the root in fig. 12, which represents a longitudinal section through a cylindrical process, is still enclosed within the tissues of the latter, and was not evident on external examina-

tion. The apex of the root was surrounded by a sheath of disorganised cells of the process. The root in the similar section (fig. 13) had already reached the surface. Vascular tissue was found in all the cylindrical processes from which roots arose, though its arrangement and the complexity of the strand differed in the various examples. Vascular tissue was also found in processes which bore no members of the sporophyte. In the specimen represented in fig. 12 the strand occupied an axial position and could be traced throughout the greater part of the length of the process. Near the base of the latter, and again towards the apex, it contained tracheides, but in the middle region they were absent; the continuity of the strand was here maintained by tissue resembling that which surrounded the tracheides in the more complex portions. The young roots, of which only one is seen, were situated in the middle third, and their steles had no direct connection with the tracheides of the vascular strand. The tissue of the process surrounding the strand was composed of cells resembling those of the prothallus and bore archegonia. In the case of the branches of the process of fig. 10, on the other hand, the tracheides of the root joined with those of the continuous vascular strand. Fig. 14 shows the structure of the latter as seen in transverse section. It resembles the stele of a root, but is simpler, and is bounded by a fairly regular sheath of large cells. This sheath was recognisable by the dense protoplasmic contents of its cells, and may be compared with an endodermis since the roots appear to take origin from it. Between the sheath and the tracheides are smaller cells with thin walls. This tissue in part corresponds to phloem, so far as its position in the strand and the fact that it is composed of elongated elements are concerned. Sieve tubes have, however, not been recognised in it.

In the above instances, the vascular strand may be fairly termed a stele, although the existence of phloem has not been established. In other processes the structure is simpler. No definite strand was present, but in the corresponding axial position groups of tracheides were found. These sometimes abutted directly upon ordinary parenchymatous cells of the process, or at places the layer adjoining them was composed of more elongated cells. Tracheides were also found near to the main group, but isolated from it by parenchyma. The differentation of the tissues of the process was thus less perfect than in the former examples, but the occurrence of roots in a corresponding position showed that the groups of tracheides and the rudimentary stele were comparable structures.

It would appear from the examples which have been referred to, that the formation of tracheides in the process is a preliminary to the development of a root, as well as of a vegetative bud from the tissues of the latter. The roots, however, although their appearance is probably to be explained on similar lines to ordinary cases of apogamy, stand to the prothallus which bears them as organs. There seems no reason to doubt that they were capable of contributing to its nutrition, and since sexual organs were present on the process, the whole organism may fairly be said to present characters intermediate between gametophyte and sporophyte.

On prothalli of a number of species of ferns, STANGE* observed, after long cultivation, peculiar conical growths on the under surface. The structure of these has been investigated by HEIM† in *Doodia caudata*, R. BR. Similar conical projections were found on some of the *Scolopendrium* prothalli. Their essential agreement with HEIM'S account of the similar structures in *Doodia* renders a detailed description unnecessary. On the prothallus represented in fig. 16, a number are seen. Here and in most cases they were clearly referable to archegonia, and even when no trace of an archegonium neck could be found, they were probably of this nature. Throughout this paper the term *archegonial projections* will be used in referring to these structures. In a case of apogamy from the culture of the variety *marginale* (fig. 8) the situation of the bud strongly suggested that its origin was to be traced to such a projection, but such a formation of numerous buds from the under surface of a prothallus as occurred in *Doodia* was never seen in *S. vulgare*.

The most striking peculiarity found in the cultures of *Scolopendrium vulgare* was the development of sporangia upon a number of prothalli of the variety *ramulosissimum*. In all the examples seen, they were situated upon the cylindrical process, usually on the upper surface, but sometimes on the side turned towards the substratum. The sporangia were associated in groups which bore a superficial resemblance to sori. In fig. 16 they are seen on the upper side of a curiously lobed process; the group represented in fig. 15 was matched by a similar group on the under side of the thick, flat process; in fig. 17 they occupy the summit of an elevation which probably corresponds to an archegonial projection, while they were closely associated with a vegetative bud in the example shown in fig. 18.

Some of the sporangia were far advanced in development and contained isolated spores with thick brown walls. The majority, however, though of normal proportions, were younger, and the development of others had been arrested at various stages. A few were found with a thicker stalk than normal, supporting an ill-formed capsule (fig. 19); these approach the imperfect sporangia which occurred frequently in the species to be next described. In fig. 20 two young sporangia at different stages are shown. They show a general similarity to normal sporangia of the same age.

The tissue underlying the groups of sporangia consists of cells, which differ in appearance from those of the rest of the prothallus. They are usually of smaller size and have more abundant protoplasm, from which chlorophyll corpuscles were absent. In this tissue evidence of recent cell division was to be detected. The contrast between the ordinary cells of the prothallus and this sub-sporangial tissue was usually sharp (fig. 21), though, when the older cells of the latter have become vacuolated, this is less striking. Cells presenting the characters just described are found in masses beneath the groups of sporangia. These groups may be of larger or smaller size and ordinary prothallus tissue intervenes between them. Frequently the

* 'Ber. d. Ges. Bot. Hamburg,' 1886, p. 43.

† 'Flora,' 1886, p. 329.

central tissue of a process consists of large cells with a thin protoplasmic lining, while the superficial layers present the characters of subsporangial tissue. In the central tissue, however, tracheides may develop, and then may be traceable into continuity with similar elements in the subsporangial tissue. In every example investigated tracheides were found in proximity to the groups of sporangia.

In connection with the projections of tissue bearing sporangia, the occurrence of archegonia in close proximity must be considered : it appears that in some cases the former stand in a similar relation to archegonia as the archegonial projections referred to above. From figs. 15–17 it will be readily seen that archegonia occur at no great distance from the sporangia. Further, when separate masses of subsporangial tissue are close together, giving on external examination the effect of a single group of sporangia, archegonia are found on the intervening areas of prothallus tissue. In such cases they are usually unopened, but with the canal and venter of a brown colour. A number of facts appear to indicate that the projections bearing sporangia are of a similar nature. That this is so in some cases does not at all exclude the probability that sporangia are also developed from tissue, the origin of which has had no connection with the site of an archegonium.

Some of the archegonia present no differences from those found in an unopened state elsewhere. But the cells around the ovum in others have, by division, given rise to a small-celled tissue, which closely resembles that found beneath sporangia, and may, in fact, be continuous with it. This may occur in connection with archegonia, the central series of cells of which has not become discoloured. Further, in some of the sporangium-bearing projections, the arrangement and appearance of the cells suggest that the projection is a modification of such an archegonium (fig. 22). In this example, what appears to be the central series of cells can be recognised. Such a case leads naturally to elevations in which all indications of archegonial origin have been lost.

The group of well-developed sporangia in fig. 17 was situated on an archegonial projection, and others which did not bear sporangia were present on the process. Beneath the sporangia, in the centre of the projection, tracheides are seen. That these elements may arise in intimate relation to an archegonium is evident from fig. 23. There an archegonium neck surmounts a projection containing a spherical group of cells, most of which had developed into tracheides. At first sight, it would appear that the group was to be traced to the ovum, but the adjoining sections of the series render it more probable that the ovum had not undergone division. The tracheides were thus developed from the cells of the venter, a region in which divisions were frequently observed to take place. The tracheides in the central region of the prothallus were continuous with the spherical group. This peculiar archegonium was situated among groups of sporangia on the process represented in fig. 15 ; on this the projection in fig. 22 was also found.

One of the groups of sporangia in fig. 16 was accompanied by two ramenta which

arched over it. This is the only instance seen in *Scolopendrium* of the association of sporangia and ramenta which was not infrequent in the next species. In the example of association of a group of sporangia with a vegetative bud (fig. 18) the former occupied the following positions :—A few were present on the shoulder of the cylindrical process, some imperfect sporangia were found just beneath the lowest ramenta of the bud, and one sporangium was inserted on the side of the narrow attachment of the bud to the tip of the process. The last archegonium that could be recognised with certainty was just behind the sporangia on the process. The most probable explanation of this specimen, the structure of which in longitudinal section is shown in fig. 24, would appear to be that within the tip of a cylindrical process tracheides developed, and on the summit a group of sporangia and a bud. Some of the sporangia remain on the process, while others have been carried up by the elongation of the insertion of the bud. Such a case may be compared with the production of two buds on the summit of a process referred to above.

In connection with the characters of subsporangial tissue, and of the cells near the border line between sporophytic and prothallus tissue in the case of vegetative buds, a fact of possible cytological interest may be recorded. In a number of these cells two nuclei were found, although no indication of a recent division was apparent. They were sometimes close together, sometimes farther apart. Cells in this state are seen in figs. 21 and 23. In the absence of evidence as to the further behaviour of these nuclei it would be premature to speculate on the possible significance of their presence.

Nephrodium dilatatum, DESV., var. *cristatum gracile*.

The original specimen of this variety of *Nephrodium dilatatum* was found wild in Carnarvon in 1870. The spores from which the cultures were made were obtained from a plant in the collection of Mr. C. T. DRUERY, F.L.S. They were sown in November, 1895, and the prothalli have been cultivated for more than two years. The latter were of the normal shape, bore sexual organs, and, when fertilisation was effected, embryos. This was the condition of the prothalli in April, 1896; three months later a number of young plants were present, the prothalli, on which they had been produced, having withered. Numerous unfertilised prothalli of considerable size and a number of dwarf male prothalli remained. The unfertilised prothalli had attained a length in some cases of more than two centimetres. They had a well-marked midrib on which numerous archegonia were situated. The necks of the latter were in some cases open, but in the majority of cases had remained closed. The central canal had in both cases undergone the usual brown discoloration.

Further departures from the ordinary form than mere increase of size were shown by a number of the prothalli. Their external form and habit will be described first; the structure and development of the different parts can then be considered in detail. In some instances a narrow flat structure proceeds from the growing point of the

prothallus; this soon broadens out and resembles the prothallus, from which it arose as a direct continuation. More commonly, however, the growth of the prothallus ceases at the apex and is continued either from the anterior margin to one side of the original growing point or from the under surface. The cells of the apical region lose their meristematic appearance, and, elongating somewhat, form a flat triangular lobe projecting into the apical depression (fig. 25). From the close agreement which this structure presents to the "middle lobe,"* developed in a corresponding situation in "aborting"† prothalli of *Pteris cretica* and *Nephrodium Filix-mas*, the same name may be applied to it. In *Nephrodium dilatatum*, however, it is not usual for the middle lobe to present this typical appearance, since one or more sporangia are frequently developed in its place.

The further growth of the prothallus may take place from the anterior margin: this may occur on one side only of the middle lobe (fig. 26) or on both (fig. 27). This last prothallus, in which the middle lobe is represented by an ill-formed sporangium, may be compared with aborting prothalli of the species described by De Bary. These growths from the margin are usually flat and prothalloid. In the more common case, however, in which growth takes place from the under surface of the cushion just behind the apex, the result is a structure to which the term cylindrical process may justly be applied on account of its usual form (figs. 28 to 31). This presents no distinction of upper and lower surfaces at its insertion, and the cylindrical form may be retained (figs. 29, 30). In the course of further growth it not infrequently assumes the flattened form (figs. 28, 32), the sexual organs being limited to the under surface. The growth from the anterior margin may also though rarely be fleshy and cylindrical (fig. 32). If the cylindrical process in *Nephrodium dilatatum* and *Scolopendrium vulgare* be compared with regard to its place of origin, it will be seen that in both it may originate from the anterior margin or from the under surface of the prothallus just behind the apex. In *Scolopendrium* the former situation is the more common, in *Nephrodium dilatatum* the latter.

Sometimes the growth of the process appears to cease, and a new growth to arise bearing the same relation to it that the first process bore to the prothallus (fig. 32). Some of the groups of sporangia appeared to occupy the apex of a cylindrical process, the growth of which had ceased in this manner. Though this view of the cylindrical process as a kind of sympodium appears to be the correct one in some instances, there are other cases which cannot be explained by it.

On the process, whether its form be flat or cylindrical, sexual organs and rhizoids occur. The former are sometimes of normal structure, sometimes more or less modified. Cylindrical processes covered with these abnormal reproductive organs not infrequently occur (fig. 34), and the latter are also found on the under surface of prothalli from which no cylindrical process has arisen (fig. 25). In the latter case they resemble the archegonial projections found in *Doodia*.

* De Bary, 'Bot. Zeit.,' 1878, p. 463.

† *Ibid*, p. 463.

Sporangia also are found in various positions on the cylindrical process. Their occurrence on the middle lobe has already been mentioned, but it will be convenient to consider in this place all the positions in which more or less perfectly developed sporangia have been observed on prothalli of *Nephrodium dilatatum*.

In the first place sporangia are found on the middle lobe. This may terminate in a single sporangium which may be well developed (fig. 30) or rudimentary (figs. 31, 27). Others may be present on the anterior margin to either side of the lobe, and this leads on to examples in which the anterior edge bears a row of sporangia (fig. 29) or becomes more strongly developed as a flat branched structure on which numerous sporangia are situated (fig. 33). Sometimes the sporangium which appears to correspond to the apex of the middle lobe can be distinguished from the rest of the group by its imperfect structure (fig. 35).

Sporangia are also found singly on the cylindrical process, but they are more commonly associated in groups. They are usually situated on the upper surface (fig. 29), though they may occur, even well developed, among the rhizoids on the side turned to the soil (fig. 36). In the only instance in which very young sporangia were seen they occupied the tip of a process. Lastly, the occurrence of ramenta in association with sporangia forming a bud-like structure must be noted. These cases, of which several have been observed, are of interest since they constitute the nearest approach to an apogamously produced vegetative bud found in the cultures of this species. The ramenta have been found clothing the tip of a process on which sporangia were developed (figs. 37, 38). In another case (fig. 39), they occurred on the under side of a narrow, flat continuation of the prothallus immediately behind the middle lobe which terminated in a sporangium.

The absence of any formation of vegetative organs of the sporophyte, except the ramenta just described in the cultures of *Nephrodium dilatatum* is, when compared with the not infrequent presence of sporangia, a striking fact, and one which must be taken into account in attempting to estimate the importance to be attached to the occurrence of the latter members.

Returning to the consideration of the structure of the different parts of the prothalli, the general habit of which has now been described and illustrated, the middle lobe may be first considered. Where typically developed, this is of triangular outline; its size varies. The example represented in fig. 40, the position of which is seen in fig. 25, illustrates the essential features of its structure. The cells of which it is composed are usually smaller than those of the rest of the prothallus. Those near the middle line are often elongated. Their clear empty appearance contrasts with the adjoining tissue of the prothallus. In the centre of the lobe tracheides are developed, forming a more or less continuous strand. When, as is not infrequently the case, the anterior margin to either side of the middle lobe presents similar characters, tracheides may also occur in these regions. The apex appears to

be occupied by a single cell in many instances, but it is impossible to state that this is always the case, especially after the lobe has reached its full size.

The strand of tracheides sometimes stops short at the junction between the colourless and chlorophyll containing tissue. Usually, however, it can be traced into the latter for a greater or less distance. When a cylindrical process arises from the under surface of the prothallus it will be seen that the tracheides reach to its place of origin. In cases where no process is present the relation of the strand of tracheides to the adjoining structures is such as to suggest a view of the nature of the cylindrical processes which originate in the position which has been mentioned above as usual in the species. In fig. 41 a small middle lobe is seen, and extending from this into the tissue of the prothallus a strand of tracheides, the position of which, as seen through a layer of cells, is indicated by the shading. At its hinder end the strand terminates beneath an archegonium, the cavity of the venter being prominent on account of the discoloration of its wall. The cells around this formed a slight conical projection from the under surface of the prothallus. Fig. 42, which represents the prothallus, from a part of which fig. 41 was drawn, enables the course of events during the growth of the prothallus to be traced. After the latter had attained a considerable size, its apical growth terminated in the formation of the small middle lobe (*a*). Growth then commenced to one side of the apex, and a cushion having formed, two archegonia, one behind the other, were developed upon it. This new growing point after a short time formed the middle lobe (*b*). It is this part of the prothallus which is seen more highly magnified in fig. 40, in which the more anterior of the two archegonia forms the conical elevation. A similar elevation, the archegonial origin of which was not so obvious, was found in a corresponding situation behind the middle lobe (*a*). Growth again started to one side of the lobe (*b*), and resulted in a continuation of the prothallus of considerable size, exhibiting a well marked midrib and equally developed wings. This was similarly terminated by the development of a middle lobe which, in this case, bears the well-formed sporangium (*c*), *and in a position corresponding to the archegonium behind* (*b*) *and the small elevation behind* (*a*), *a cylindrical process of considerable size was formed.*

In connection with this subject, and before passing to the consideration of the structure of the typical cylindrical process, some of the modifications which the sexual organs of these prothalli underwent under conditions of culture which prevented the completion of their normal development may be referred to. This can be done with the greater brevity since some of the resulting structures closely resemble those figured and described in *Doodia caudata*.* Thus small conical projections and intermediate forms between them and normal archegonia were frequently observed.† A projection of a slightly different form, the archegonial nature of which is however obvious, is

* HEIM, 'Flora,' 1896, p. 329.

† HEIM, *loc. cit.*, p. 337, fig. 5.

shown in fig. 43. This projection, which originated by the division of the cells surrounding the ovum of a young archegonium, may be compared with fig. 44, which represents a similar projection developed just behind the apex of a prothallus. Such a conical projection as this leads directly to the smaller cylindrical processes (compare fig. 42).

The formation of conical projections of this sort is not the only modification which archegonia were found to undergo. In the case of the archegonia crowded together on such a cylindrical process as those seen in fig. 34, the surrounding cells took little or no part in the new growth. This proceeded mainly from the neck of the archegonium, though within the venter, which often projected above the surface of the prothallus, a tissue of peculiar appearance was frequently found. A case of slight growth of the cells of the neck is seen in fig. 45. In the archegonium represented in fig. 46, however, growth of this sort has resulted in a three-rayed structure, each branch being to all appearance capable of continuing its growth. Growths of very various form having a similar origin were found.

The archegonium which in fig. 47 is seen surmounting a projection from the surface of a cylindrical process exhibited a still more peculiar deviation from the normal. Within the canal of the neck, which had not opened, and in the position of the neck canal cell two small tracheides were found side by side. This is the only specimen of the kind which has yet been noticed. It may be noted that tracheides were present in the substance of the cylindrical process which bore the archegonium, and a group of sporangia was situated upon it.

The antheridia also became modified in different ways. In some cases the central cell of an antheridium would cease to develop and become discoloured, while the cells of the wall took on active growth. At other times projections resulted which resembled those of *Doodia.** In the centre of these was a small celled tissue, the origin of which could be traced to the cell from which the spermatozooids are normally derived. A somewhat similar tissue, the cells of which were densely filled with protoplasm, sometimes occupied a central position in projections of archegonial origin. Whether this was derived from the cell which would normally have formed the ovum and other cells of the central series is not certain. In some cases it seemed probable that such was its origin at least in part, but in other projections (fig. 43) a similar group is found although the central series of cells has taken no part in its production.

The structure of some of these modified archegonia is of interest for comparison with that of well-developed cylindrical processes. The latter may consist wholly of parenchymatous cells resembling those of the rest of the prothallus. Frequently one or more groups of tracheides are present in a central position, and occasionally the whole length of the process is traversed by a vascular strand. Even where this is absent a difference may be observed between the central and peripheral cells. The existence of a definite central tissue, whether developed as tracheides or not, cannot

* HEIM, *loc. cit.*, fig. 3.

however be considered usual. The frequency with which the process assumes the flat prothalloid form in the course of further growth is an additional reason for regarding the presence of tracheides in it as the first indication of apogamy.

The situations in which sporangia occur have been already mentioned; it remains to consider the structure of the sporangia themselves, and their relation to the underlying tissue. In fig. 48 the most perfectly developed group of sporangia which has been seen is represented. It was situated on a slight elevation near the base of a thick cylindrical process which sprang from the anterior margin of a prothallus by the side of the middle lobe. The latter bore an imperfect sporangium, which is seen to the right of the process in the figure. The group consisted of eight nearly ripe sporangia. These agreed in structure with normal sporangia developed on the sporophyte. Their stalks were thin, and the wall of the capsule was well developed. The cells of the annulus had the inner walls and those between adjoining cells thickened, and of a reddish-brown colour. The spores were far advanced in development, but not quite ripe; they had a fairly thick brown wall and a single nucleus could be detected, but granular remains of the tapetum were still present around them. The thin flat structure composed of colourless cells which arises close to the group is probably a ramentum, though less perfectly developed than the others which have been mentioned above.

The behaviour of nearly ripe sporangia with reagents showed that the mechanism of dehiscence was capable of acting normally. This might indeed have been inferred from the perfect structure of the sporangium wall. The spores in the sporangium of fig. 30 were larger than those shown in fig. 48. A slight amount of granular matter still remained around some of them; besides this, smaller bodies with a dark wall were present between the larger spores. These were probably spores, the development of which had been arrested. Some of those spores are drawn in fig. 49, *a*; fig. 49, *b*, shows a single ripe spore from the sporophyte drawn to the same scale.

The number of spores contained in these sporangia appeared to agree in most cases with that commonly found in sporangia removed from the plant from which the culture was made. In some cases fewer well developed spores were found, but the occurrence of arrested spores readily explains this variation.

The structure of a group of spores from a sporangium is shown in fig. 50. The cell contents appeared healthy.

From what has been said as to the appearance and structure of the spores developed upon the gametophyte, it will be apparent that some of them might probably have been capable of germination. The few attempts made have been unsuccessful. Very little importance, however, can be attached to this negative result, since, in all the cases, from the difficulty of obtaining ripe sporangia, the spores sown were in a less mature condition than those seen in fig. 49. Since 1896 the prothalli of this culture, which are still under observation, have ceased to bear sporangia, and further attempts at germination have been impossible. The interest which would attnch to the proof

of their capability of germination is obvious, and will be referred to in the theoretical discussion of results.

It has not been found possible to trace the development of the sporangia in detail. From the stages which have been observed, however, it is highly probable that in the case of the well-formed sporangia it is in the main normal. The youngest sporangium yet found is shown in fig. 51. Although slightly shrunken, it is obvious that the divisions have as yet succeeded one another much as in a normal sporangium, although there are differences of detail. Development may be arrested at any stage, and not infrequently the contents of the capsule are found to be less advanced than the appearance of the wall had rendered probable.

When the conditions under which these sporangia developed are borne in mind, it will not appear strange that so many cases of arrest were met with ; the wonder is rather that such perfect sporangia are ever found. But in addition to the normal sporangia of various ages, others were found which from the beginning differed from those borne by the sporophyte, and may be looked upon as imperfect in a different sense to those in which normal development is simply arrested. These may be met with in any of the situations in which normal sporangia occur, but are most frequently seen representing the middle lobe or situated upon it. (Figs. 26, 27, 31.) Fig. 52, which represents the sporangium borne upon the middle lobe of the prothallus seen in fig. 27, will serve to illustrate the main characters of these imperfect sporangia. They have a thick short stalk, a globular head, the cavity of which may contain spores, or more commonly, appears empty, and their wall rarely shows any indication of an annulus. Tracheides are in nearly all cases found in the stalk just below the head, and they may extend back for some distance. In fig. 52 their position is indicated by the shading of this region of the stalk.

The structure of the ramenta need not be considered in detail since they agree with those found on the sporophyte. Their form is, however, somewhat irregular.

In *Scolopendrium* it has been seen that the tissue beneath a group of sporangia presented characters which distinguished it from the adjoining cells of the prothallus. It becomes of importance to decide in what degree this holds for *Nephrodium dilatatum*. It may be stated generally that while the underlying tissue is always recognisable, the line of demarcation is usually not sharp as in *Scolopendrium*. The contrast, when it exists, is dependent upon different characters of the cells in the two species. The tissue beneath sporangia, which are situated on the anterior margin of the prothallus, is always found to be composed of cells like those of the middle lobe. In the majority of these cases this tissue is directly comparable with the latter structure. Tracheides are found in it as was seen to be the case for the typically developed middle lobe. Their position and relation to the cylindrical process is indicated in fig. 53, in which a number of sporangia occupied the position of the middle lobe. In fig. 54 a strand of peculiar cells is indicated beneath the single

sporangium. This is one of the few cases in which typical tracheides were not found associated with a sporangium.

When sporangia are situated on the cylindrical process, tracheides were always found in the underlying tissue. The subsporangial tissue was usually distinguished by its smaller cells which did not contain chlorophyll. In this, its cells resembled those of the middle lobe. Fig. 55 represents a longitudinal section through the tip of the process in fig. 38. In the tissue beneath the ramenta and sporangia there is a group of tracheides.

The question arises whether any relation can be traced between the sporangia and sexual organs. While a comparison of the abnormal archegonia described above and the imperfect sporangia suggests the possibility of the development of a sporangium from an archegonium neck, the facts as yet observed do not permit of any satisfactory conclusion. The usual position of the imperfect sporangia would be difficult to explain on any such view.

The two preceding species have been described in considerable detail, since some of the departures from the normal which they present are of special interest. The behaviour of other cultures will be described more briefly, only those results which possess a theoretical interest being dwelt upon. This method of treating the subject is facilitated by the general similarity of the phenomena in the different species.

Nephrodium Oreopteris, Desv., var. *coronans*, Barnes.

The prothalli were at first of normal shape, though, on account of the almost vertical position which many of them assumed, the general aspect of the culture was peculiar. A few normal embryos were produced. The prothalli became elongated, and a thick midrib was formed by periclinal divisions of the cells of the cushion. Gametophytic budding from the margins and the thick anterior end, occurred in a considerable number. Others bore archegonial projections which attained a considerable size, and in appearance and structure corresponded to those of *Doodia*.

From other prothalli, a cylindrical process arose, usually as a direct continuation of the apex, but sometimes from the under surface just behind it. The processes attained a considerable length, and in appearance and structure resembled those of *Scolopendrium vulgare.* In some a distinct axial strand, containing tracheides, was present.

Others presented a further step in the direction of sporophytic structure, in that ramenta developed upon them. In fig. 56, a single ramentum is seen on the side of the process near the tip, while on other prothalli several ramenta were borne. The prothallus, represented in fig. 57, is of interest for comparison with the other examples. The two outgrowths on the process resemble ramenta in position and shape, but their cells were similar to those of the prothallus, and quite different from the empty-looking tissue of a ramentum. The structure of the processes which bore

ramenta was, unfortunately, not ascertained, but it may reasonably be supposed that a vascular strand was present, since tracheides were found in other cylindrical processes of this species.

Aspidium aculeatum, Sw., var. *multifidum*, Woll.

The soil on which the prothalli of this species grew, was better drained than that of most of the other cultures and remained drier. The aspect of the prothalli and the frequency of gametophytic budding appeared to stand in relation to this. Embryos were produced on the few prothalli which became fertilised. The unfertilised individuals became elongated, their thin marginal portions were thrown into folds, and as they became older, the whole prothallus assumed a deep brown colour. Many of the rhizoids were short or remained almost undeveloped. Numerous archegonia were situated on the midribs, and antheridia were also present, especially on the small prothalli which arose by gametophytic budding. Most of the archegonia underwent no further development; in many cases they never opened. From others, archegonial projections were formed.

Gametophytic budding took place freely; after two years, the position of each of the original prothalli was indicated by a group of small green prothalli which had arisen in this way. It sometimes proceeded from the margin, but usually from the under surface of the mid-ribs. Now and then an archegonium neck grew on as a prothallus,* but any superficial cell or group of cells, although their walls had assumed a brown colour, appeared capable of taking on new growth. Frequently, the young prothalli were grouped round a central point (fig. 58), and in some at least of these cases, the budding was found to proceed from an archegonial projection. The latter sometimes grew on into a structure comparable to a cylindrical process, but which soon assumed the flat prothalloid form (fig. 58). On the under surface of a few prothalli, a slightly different growth took place: a number of cells divided repeatedly parallel to the surface, and gave rise to a flat elevation of considerable extent. The cells of which this was composed were small and meristematic, and thus differed from those of the gametophytic buds, which resembled the tissue of the prothallus. The few examples of apogamy found in this culture appeared to owe their origin to such small-celled outgrowths. One of them is shown in fig. 59. The young sporophyte is peculiar, in that the successively-formed leaves have all retained the simple form of the first leaf. This occurred in others of the apogamously-formed sporophytes, but not in all. Its explanation is probably to be looked for in the deficient nutrition of the young plant;† in this connection, attention may be called to the poorly-developed root of the sporophyte figured. The tissue of the sporophyte was continuous with

* Compare Goebel, "Sigber d. Math. Phys. Cl. d. k. Bayer. Akad. d. Wiss.," vol. 26, p. 475, *et seq.*

† Compare Goebel, *ibid.*, p. 479.

that of the prothallus, but on account of the brown colour of the latter, the division was well marked.

In a few prothalli tracheides were found. Their situation was usually at the junction between a new growth and the original prothallus.

Aspidium angulare, WILLD.

The spores of two varieties of this sub-species of *Aspidium aculeatum* were sown. The differences in form and in behaviour, on long cultivation of their prothalli, were such as to necessitate separate description; these differences cannot be ascribed with certainty to any difference in the conditions.

A. angulare, var. *foliosum multifidum*.

The prothalli in this culture were numerous and closely crowded; most of them remained small, and many bore antheridia only, or in addition a few archegonia. Only a few normal embryos were produced. Eight months after the spores had been sown a large proportion of the prothalli became apogamous. The buds were formed from the anterior margin, or close behind it, from the under surface. Frequently two or even three buds were formed on a single prothallus of small size. Fig. 60 represents a common case; of the two buds, which are both in an early stage, one has arisen from the under surface while the other occupies the margin. Behind the former bud an archegonial projection is seen. From this and other specimens it appeared probable that the buds which arose from the under surface occupied the position of archegonia. This explanation cannot, however, be extended to apogamous developments from the margin. The buds rapidly developed into young plants. The order of appearance of the different members agreed with that usual in *Pteris cretica*. The first leaf was the result of the growth of the rudimentary bud; on it, shortly after it had become recognisable, the stem apex appeared, and with the growth of the stem leaves, which showed a progressive complexity of outline, were developed. Sometimes the leaf alone developed, and in other examples the first leaf and the stem apex appeared as separate elevations side by side on the prothallus.

Sections through the buds showed the continuity of the tissues of the prothallus and sporophyte. Usually no tracheides were found in the gametophyte itself, though they appeared in the attachment of the bud. In connection with the possible relation between the buds and archegonia, the structure shown in fig. 61, is of interest. This was situated just where the prothallus continued into a bud, which had formed from the apex. The neck of the archegonium projected above the surface, but in its withered state it was impossible to decide whether it had opened or not. Within the venter the ovum is seen divided into three cells. It is impossible to state definitely that this division did not follow fertilisation, but the fact that a

bud developed apogamously, and the absence of normal embryos from the rest of the culture, render this improbable. Further, the fact that a group of small cells occupied a similar position further back, on the same prothallus, lends weight to the view that the division of the ovum had occurred independently of sexual fusion.

Besides numerous examples of the apogamous development of a normal sporophyte, this culture yielded a number of prothalli in which the characters of the two generations appeared more intimately mixed. Isolated ramenta occurred on the gametophyte; in fig. 62 a single ramentum is seen on the under surface of a prothallus which also bears a bud. In the example represented in fig. 63 two large ramenta were situated on the anterior margin. They stood on either side of the base of a narrow, flat continuation of the prothallus, which terminated in a bud. Since sexual organs and rhizoids were absent from this intermediate region it must be regarded as approaching the sporophyte in structure though no tracheides were found in it.

Another point of interest is the occurrence of new growths, which assume the characters of the sporophyte, and then continue their growth as prothalloid structures on which sexual organs develop. In the case of the prothallus, represented in fig. 64, the new growth corresponded in its place of origin to one of the apogamously-produced buds; on it a number of ramenta developed, but from the region where they occurred it assumed the flattened form. A few tracheides were found in the structure. The appearance left little doubt of the gametophytic nature of the flat portion, but this was certain in another example (fig. 65). Here growth from the margin of the prothallus had taken place. The structure was at first narrow, but widened and became irregularly lobed. The growing point resembled that of a prothallus, and rhizoids and a few archegonia were present on the under surface. But the narrow region resembled a leaf-stalk; it bore a ramentum, and a central strand was present, the vascular nature of which was shown by the existence of a single spiral tracheide. These examples suggest a comparison with some cases of apospory from the leaves of young plants.

A. angulare, var. *acutifolium multifidum.*

This culture presented a striking contrast to that of the preceding variety. The prothalli, which bore numerous sexual organs, grew to a considerable size; a few produced normal embryos, but the majority remained unfertilised. A few became thick and fleshy, archegonia were produced on the upper as well as the lower surface, and a structure approaching a cylindrical process resulted. The majority, however, remained of normal texture, and, after increasing considerably in size, ceased to grow. New growths appeared in positions corresponding to the buds in the preceding variety, but these, in all cases, assumed the form of prothalloid branches. Changes occurred in the sexual organs, of the same nature as those

referred to in most of the species investigated; all stages between normal archegonia and archegonial projections of considerable size were met with. This and other points of agreement render it not improbable that further cultivation may induce apogamy in these prothalli. The results so far, however, have been negative.

Athyrium niponicum, METT.

Spores from normal and crested plants of this fern growing in the open air at Kew were sown. The results will thus aid in estimating the importance to be attached to the cresting of the sporophyte as a cause of apogamy and, though the differences are but slight, will be described separately for the two cultures.

A. niponicum. Normal form.

The cultures resembled that of *Aspidium aculeatum*, in that the prothalli soon assumed a brown colour; some resemblance in the results on long cultivation will also be apparent.

New growths originated in different situations. Sometimes a narrow, flat continuation of the apical region was present, or similar structures arose from a number of points on the anterior margin of the prothallus. These gametophytic buds sometimes branch dichotomously and, in the frequent absence of sexual organs, further depart from the common structure of marginal growths. They may, however, come to resemble ordinary gametophytic buds as growth proceeds. At other times filamentous prothalli, which develop into flat spathulate structures, arise from superficial cells of the under surface. But the most interesting growths from the under surface arose in connection with archegonial projections. A number of the latter, from one of which a flat prothalloid growth of considerable size had proceeded, are represented in fig. 66. This appeared to be a case of gametophytic budding from a structure which, in other species, may develop into a sporophyte, and the structure of the prothalloid outgrowths in most instances confirmed this view. But in others, that shown in fig. 66 for example, although sexual organs were borne upon the prothalloid continuation of an archegonial projection, the latter approached the sporophyte in its structure. A vascular strand containing a number of well-developed tracheides was present in the stalk-like region of the out-growth, although they were not found in the original prothallus. These structures may be compared with the cylindrical processes of prothalli of *Nephrodium dilatatum*, and in this case, also, the appearance of tracheides may be considered to be the first indication of apogamy. Occasionally the apical region of the prothallus grew on to form a structure resembling the form of cylindrical process common in *Scolopendrium*, both in position and structure (fig. 67). Apogamously-developed buds have not yet been observed in this culture.

A. niponicum, var. *cristatum.*

The general aspect of these prothalli agreed closely with that of the preceding culture. Normal embryos were produced rather more abundantly. Later gametophytic budding resulting in filamentous or flat prothalli took place from the margin or the under side. Well marked archegonial projections were formed (fig. 68). As was seen in fig. 66, one of these projections has grown into a cylindrical process which soon became prothalloid. In a similar growth from another prothallus tracheides were present. Besides this indication of apogamy the development of a few of the young plants in this culture was found to be apogamous. Little importance can however be attached to their presence in the culture of the crested variety and absence from that of the normal form, in view of the similarity which in other respects existed between the two cultures.

Aspidium frondosum, LOWE.

The apogamous prothalli of this fern were discovered on examining sowings which had been made in the pits at Kew. To the kindness of the authorities of the Royal Gardens I owe the opportunity of examining a number of them in detail. The account of the result is placed with the description of the cultures made under known conditions, since those to which the prothalli of *Aspidium frondosum* had been accidentally exposed were essentially similar.

When first noticed the prothalli were of large size, some being more than 2 centims. in length by 1 centim. broad. They were attached to the ground by numerous rhizoids, among which archegonia were present in large numbers. No normal embryos or young plants developed from them were present in the pot. On several of the prothalli, however, apogamously produced buds were visible: sometimes there was only one, but more commonly several. In the case of the prothallus, represented in fig. 70, no fewer than six buds at about the same stage of development were present. They terminated short, thick cylindrical processes which originated from the anterior margin or just behind it. The mode of origin of the sporophyte agrees closely with what was described for *Scolopendrium.* The smooth, rounded tip of the process becomes of a lighter tint than the region behind, ramenta then develop and soon cover the apex completely. Very soon after this the first leaf becomes apparent.

In structure the similarity to the case of *Scolopendrium* was maintained. A vascular strand developed in a central position surrounded by prothalloid tissue; this strand was continuous with the procambium of the bud. Between the tissue of the latter and that of the process a well-marked line of junction, which ran almost transversely, was visible. This contrast was due to the smaller size and slightly different contents of the sporophyte tissue.

The condition of things above described existed in this culture in August, 1896. When it was again examined five months later the appearance presented was wholly different. Most of the prothalli had an embryo attached to the under surface, and these and the young plants in the culture were all of normal structure and mode of origin. No further apogamous developments had occurred. The change in the behaviour of the prothalli was explained by the fact that, previous to August, 1896, the culture had not been watered from above. To this the large size of the prothalli and the cases of apogamy stood in direct relation. Shortly after the date mentioned the prothalli were regularly watered: as a result fertilisation ensued, and the development of the young plants checked the growth of the prothalli and their tendency to the apogamous production of buds.

Athyrium Filix-fœmina, BERNH.

The three varieties, *coronatum*, *cruciato-cristatum* and *percristatum*, of this species were sown. Normal embryos were borne on a large number of the prothalli, an occurrence which reduced the number subjected to long cultivation, and accounts for the comparatively few examples of apogamy. Those prothalli which had remained unfertilised, however, underwent similar changes to those seen in the preceding species. As in these archegonial projections occurred. They were numerous and well developed, and frequently exhibited a distinction between the central group of cells and the peripheral layers. The former was composed of smaller cells with dense contents which, in some cases, though not in all, appeared to be referable to the central series of cells of a young archegonium. Outgrowths of larger size, which corresponded to the cylindrical processes already mentioned in their form and structure, were found to arise from the apex or from the lower surface of some of the prothalli. They contained tracheides, especially when a sporophyte had been produced upon them apogamously. These elements were usually isolated or in small groups and did not form a definite vascular strand in any of the examples yet examined. Their position is indicated in fig. 74.

The most frequent position of apogamously-produced buds was as a prolongation of the apical region (figs. 70, 71); indications of their origin from archegonial projections were also observed. The order of appearance of the first leaf and the stem apex was not determined, but, as is usual in young plants originating in this manner, the appearance of the first root was delayed until several leaves had become unfolded. Fig. 71 represents a similar case; tracheides are seen to be present in the flat continuation of the apex which bore a single leaf, and on the side of it a projection which corresponded to the stem apex. In the example shown in fig. 72, the latter portion of the sporophyte was not represented, and the cylindrical process, which arose from the under surface of the prothallus, continued its growth as a leaf stalk. On the basal portion small prothalloid lobes were borne, but these were

replaced by ramenta on passing to the leaf stalk in which a definite vascular bundle was present. This did not appear until the intermediate region between the gametophyte and sporophyte, tracheides being absent from the prothallus itself.

It is impossible to avoid raising a question with regard to the apogamous development of buds in this species, which some specimens from the present cultures suggest, though they do not settle it. Young plants have been seen, the endogenous origin of which appears beyond doubt; in some examples the boundary between sporophyte and gametophyte was a fairly regular one, but in others the tissue seemed continuous. Further, as in the example shown in fig. 73, tracheides may be present in the underlying portion of the same prothallus. Careful examination of a number of instances of this kind leads me to the opinion that the probability of an apogamous development taking place within the tissue of the prothallus, and, when the superficial layers have been broken through, simulating a normal embryo must be borne in mind. Whether such developments will be traced to an unfertilised ovum, as the structure of some archegonial projections suggests, must be left undecided until further observations have been made. The structure contained within the elevation far back on the prothallus in fig. 70 might be explained in this way, but it possibly represented an embryo arrested in an early stage of development.

The observations described above establish the possibility of inducing apogamy in *Athyrium Filix-fœmina*; this was previously highly probable from an observation recorded by Mr. DRUERY* on an aposporously-produced prothallus of the variety, but in that isolated case the structure was not investigated.

Polypodium vulgare, var. *grandiceps*.

This culture had a characteristic aspect from the deep green colour of its prothalli, the thin margins of which became thrown into folds. From the under surface thick reddish brown rhizoids were produced. The numerous archegonia had their necks almost always closed, a fact which points to the successful exclusion of fluid water. Only one or two normally-produced plants originated in the pot, and with these exceptions the prothalli were grown for eighteen months before any noteworthy change occurred. About this time (June, 1897), gametophytic budding was noticed. This took place sometimes from the margin, at other times from the under surface. When in the latter position it resulted in the appearance on the mid-rib, or more commonly just within the margin, of filamentous growths, which soon widened into prothalli of spathulate outline. This profuse gametophyte budding stands in direct relation to the apogamous development of sporophytes, the first examples of which were noticed at the same time; numerous instances occurred in the six months following.

Sometimes the bud forms as a continuation of the prothallus apex (fig. 74). In

* 'Gardener's Chronicle,' Nov. 10, 1894.

these cases the bud soon becomes covered with ramenta, and the rudiments of stem and first leaf appear almost simultaneously. They resemble buds of *Scolopendrium* in external appearance. In other cases the apex of the prothallus continued as the first leaf, on the side of which near its base the apex arose. Such a case explains the occurrence of structures to some degree intermediate between prothallus and leaf in this position (fig. 76). In these cases, several of which were examined, the prothallus continued as a narrow strap-shaped body. This did not bear sexual organs, which were abundant up to its point of origin. The hairs upon it, which resembled those on a young leaf stalk, and the occurrence of intercellular spaces afforded evidence of its sporophytic nature. Stomata, however, were not found in the epidermis, and a vascular strand has not been recognised, though tracheides were sometimes present at the point of origin from the prothallus.

Other buds were inserted on the under surface near the margin or on the margin itself (fig. 75). In both these situations they may co-exist with gametophytic buds, and, indeed, the region by which they were attached to the prothallus agreed exactly with the adjoining prothalloid growths, and must be considered to be of this nature. Only now and then were buds found seated directly on the prothallus; in the majority of cases the stalk which connected them to it was only a few cells in thickness, and sometimes was a simple filament. In connection with the relation which existed between gametophytic budding and apogamy in this species, the simultaneous production of a number of young sporophytes from the same prothallus may be mentioned. No instance of the formation of archegonial projections or of buds in the position of these structures was seen; this is a point of difference between this culture and those of all the other species in this series of cultures. It is unnecessary to describe the structure of these apogamously-produced buds in detail, since it agrees essentially with the changes observed in other species on the transition from tissues of the gametophyte to those of the sporophyte. As a rule tracheides were absent from the original prothallus, but appeared in the base of the bud itself.

Nephrodium Filix-mas, Sw.

Apogamy was discovered in the variety *cristatum* of this species by DE BARY.* Later KNY† recorded it for prothalli derived from spores of an uncrested plant. The existence of descriptions of the form of apogamy most frequent in this species renders a detailed account based on these cultures unnecessary. The very different behaviour manifested by the prothalli of the different varieties sown will, however, be briefly described, and the more important points illustrated.

In this country three sub-species of *N. Filix-mas* are sometimes distinguished (under the names *N. Filix-mas*, *N. pseudo-mas*, and *N. propinquum*) and it has been

* 'Botanische Zeitung,' 1878, p. 470.

† 'Entw. von *Aspidium Filix-mas*, Sw.,' Berlin, 1895.

suggested that their prothalli might be found to behave differently as regards the occurrence of apogamy.* When the cultures of this fern were made, it appeared advisable to investigate normal and crested forms of these three sub-species: material for the purpose was kindly supplied by Mr. DRUERY. I find however, after repeated attempts, that I am unable to distinguish these sub-species with certainty, and have accordingly arranged the results in the accompanying table so as to afford a comparison between crested and uncrested forms. The names of the sub-species are given in the table on the authority of Mr. DRUERY for convenience of reference, though I am not prepared to lay stress on the distinction.

RESULT of Cultures of Crested and Normal forms of *Nephrodium Filix-mas.*

Name.	Immediate Result.	Result after long cultivation.
UNCRESTED FORMS:—		
N. propinquum	Normal embryos	Gametophytic budding Archegonial projections Cylindrical processes
N. pseudo-mas	Apogamy	
CRESTED FORMS:—		
N. propinquum, var. *cristatum*	Normal embryos	Gametophytic budding Archegonial projections Cylindrical processes
N. pseudo-mas, var. *cristatum*	Apogamy	
N. pseudo-mas, var. *polydactylum*, WILLS	Apogamy	
N. pseudo-mas, var. *polydactylum*, DADDS	Archegonial projections Apogamy	
N. Filix-mas, var. *crispato-cristatum*	Apogamy	
N. Filix-mas, var. *polydactylum cristatum*	Apogamy	
N. Filix-mas, var. *cristatum* Uncrested frond Crested frond	Normal embryos	Gametophytic budding Archegonial projections Cylindrical processes Apogamy

From the above table it appears that no relation can be traced in this series of cultures between the cresting and apogamy. This will be discussed in a subsequent section, but the behaviour of the several varieties will be here described, and set in relation to the preceding species. With regard to the completeness of apogamous reproduction, the different forms investigated fall into three groups.

(1.) The prothalli are capable of bearing normal embryos; if unfertilised they

* DRUERY, 'Gardener's Chronicle,' August 24, 1895.

undergo the usual modifications of form and structure, which in one case culminated in apogamy.

(2.) Sexual organs are usually produced, but no normal embryos occurred. Archegonial projections arise, from one of which the sporophyte is produced apogamously.

(3.) The prothalli do not bear archegonia. After attaining a certain size a bud arises apogamously on the under surface.

The first class included *N. propinquum*, normal and crested, and *N. Filix-mas*, var. *cristatum*. The latter was a slightly or irregularly crested form, found wild at Kilrush, and spores from crested and uncrested fronds were sown for purposes of comparison. No difference was, however, evident between the prothalli, and the two cultures will be described together.

N. Filix-mas. (Kilrush plant.)

The prothalli, which were at first of normal shape, contrasted with apogamous ones of the same species in adjoining cultures, by their greater size, thicker cushion, and deeper green colour. Having been watered from above, many normal embryos developed. Subsequently the possibility of fertilisation was guarded against, and the remaining prothalli were kept under observation for eighteen months. The changes which these unfertilised prothalli underwent were of a similar nature to those described above for other species. In some, simple increase in size with occasional dichotomous branching took place; the mid-rib became thick as the result of frequent periclinal divisions in the superficial cells. Some of the prothalli continued their growth as a narrow thick lobe of considerable length (fig. 77), which became almost cylindrical at parts, and resembled a form of old prothallus frequently found in *Scolopendrium vulgare*, var. *marginale*. Not infrequently distinct archegonial projections resulted from the growth of cells around and beneath the ovum (fig. 79). Other growths from the under surface deserve the name of cylindrical processes. On the one shown in fig. 77, a ramentum was situated laterally; in the substance of this process tracheides were found. This is the only example of apogamy induced by long cultivation which I have yet observed in *N. Filix-mas*. The occurrence is of interest as indicating that under prolonged cultivation prothalli of this species which are capable of sexual reproduction, would probably behave in a smaller way to those of the species described above. Unfortunately these cultures were destroyed after a year and a half.

Nephrodium propinquum. Normal and Crested.

The cultures closely resembled those just described. While the same modifications of the form and structure of the prothallus were called forth by prolonged cultivation, no case of apogamy has yet been found.

N. pseudo-mas, var. *polydactylum*, DADDS.

This is the only form investigated which comes under the second type, as distinguished above. On this account it is of special interest, since it serves to connect such specialised cases of apogamy as those first described by DE BARY with the induced apogamy which has been shown to occur in one of the preceding varieties. The prothalli resembled in form and texture the apogamous prothalli on which no archegonia are produced. A considerable proportion of them indeed produced at once a bud (fig. 79), thus agreeing with the only form of apogamy seen in the varieties which have yet to be mentioned.

Upon about one half of the prothalli, however, archegonia were borne. Antheridia, as is usual in apogamous prothalli of this variety, were present, but no instance of a normal embryo being formed was met with. It would appear probable that this was due to the incapability of the archegonia to be fertilised, for the spermatozooids, when liberated from the antheridium, were capable of active movement and appeared to be normal. The archegonia were at first of normal appearance, but later gave rise to characteristic archegonial projections (fig. 80). A number of these sometimes formed one in front of the other, until at length a vegetative bud was developed. This was always situated nearest to the apex of the prothallus (figs. 80, 81, 82). It was sometimes formed from the side of a projection which bore an archegonium neck (fig. 80); more commonly the projection which gave rise to the bud showed no trace of its origin save by the similarity of its position to the typical archegonial projections (figs. 81, 82). As the growth of the bud proceeds, the projections behind it may appear to be raised upon its sides. The series of examples in this culture demonstrated the relation of the apogamously-produced bud to an archegonium. In connection with this it is of interest to note that from the first discovery of apogamy such a relation has been looked for.*

The remaining varieties of *N. Filix-mas* investigated, *N. pseudo-mas*, crested and uncrested, *N. pseudo-mas polydactylum*, WILLS, *N. Filix-mas polydactylum cristatum*, and *N. Filix-mas crispato-cristatum*, agreed in being exclusively apogamous. No archegonia or archegonial projections were found on the prothalli, though occasional antheridia were present. Detailed description is unnecessary, since the prothalli presented no difference from the structure and development described by DE BARY and KNY.

COMPARATIVE TREATMENT OF RESULTS.

In the preceding pages the results of cultivating prothalli of nine species of Leptosporangiate Ferns for a period of more than two years have been described in detail. Excluding *Nephrodium Filix-mas* (the behaviour of the different forms of which has been analysed in a table above), the results obtained are summarised in Table II. To

* Compare FARLOW, 'Q. J. M. S.,' 1874, p. 268.

this, *Aspidium frondosum* is appended, since its abnormal developments have been shown to depend upon similar modifications of the conditions of life to those to which the other species were exposed.

TABLE of the Results of cultivating Prothalli for a period of two years and a-half.

(NOTE.—In every species normal embryos were produced when conditions permitted fertilisation.)

Name.	Result.
Scolopendrium vulgare, SM. var. *ramulosissimum*, WOLL.	Gametophytic budding. Development of archegonial projections. Development of cylindrical process, usually from the apical region of the prothallus. Apogamy . { Tracheides in cylindrical process. Leaves, roots, and ramenta on process. Sporangia on the process. Vegetative buds from tip of cylindrical process, or in place of an archegonial projection.
var. *marginale*	Similar to var. *ramulosissimum*, but no sporangia, isolated ramenta, or leaves found.
Nephrodium dilatatum, DESV. var. *cristatum gracile*	Gametophytic budding. Development of archegonial projections. Development of cylindrical process, usually from the under surface just behind the apex, which formed a "middle lobe." Apogamy . { Tracheides in middle lobe and cylindrical process. Sporangia, sometimes associated with ramenta, on middle lobe and process. No vegetative buds.
Nephrodium Oreopteris, DESV. var. *coronans*, BARNES	Gametophytic budding. Development of archegonial projections. Development of cylindrical process from apex of prothallus. Apogamy . { Tracheides in process. Ramenta on cylindrical process. Vegetative buds (rare).
Aspidium aculeatum, SW. var. *multifidum*, WOLL.	Gametophytic budding. Development of archegonial projections. Apogamy . { Tracheides in prothallus. Vegetative buds (rare).
Aspidium angulare, WILLD. var. *foliosum multifidum*	Gametophytic budding. Development of archegonial projections. Apogamy . { Ramenta on prothallus. Vegetative buds (frequent).
var. *acutifolium multifidum*	Gametophytic budding. Development of archegonial projections. No apogamy seen.
Athyrium niponicum, METT. Normal form	Gametophytic budding. Development of archegonial projections. Apogamy . { Tracheides in prothalloid growths from archegonial projections.
var. *cristatum*	Similar to the normal form, but in additon a few apogamously-produced vegetative buds.

TABLE of the Results of cultivating Prothalli for a period of two years and a-half—(continued).

Name.	Result.
Athyrium Filix-fœmina, BERNH . . var. *percristatum*, COUSENS . . var. *cruciato-cristatum* . . . . var. *coronatum*, LOWE	Gametophytic budding. Development of archegonial projections. Development of cylindrical process from apex, or from under surface of the prothallus. Apogamy . { Tracheides in process. Continuation of process as a leaf. Vegetative buds.
Polypodium vulgare, L. . . . . var. *grandiceps*, FOX	Gametophytic budding. Apogamy . { Isolated leaf-like growths. Vegetative buds (numerous).
Aspidium frondosum, LOWE (from the pits, Royal Gardens, Kew)	Apogamy . { Vegetative buds produced on short cylindrical processes before the culture had been watered. After the culture was watered, normal embryos.

The statistical aspect of this table of results first demands attention. Excluding *Aspidium frondosum*, the striking result becomes apparent that of eight species of ferns which were only known to be reproduced in the normal manner all were induced to become apogamous under conditions which rendered fertilisation impossible. In some it is true the instances of apogamy were few, but in others (*Scolopendrium vulgare, Nephrodium dilatatum, Aspidium angulare, Polypodium vulgare*) they were numerous. It is probable that with a slight variation in the conditions a similar supply of apogamous prothalli could be obtained from the species which in the particular cultures under consideration only yielded a few examples. Besides this agreement in the ultimate result, the similarity in the other results of prolonged cultivation is worthy of note. In all, as might have been anticipated, more or less profuse gametophytic budding of the ordinary kind occurred. But besides this, other changes, which, in some instances, led directly to the apogamous developments, were noted. Thus in all, with the exception of *Polypodium vulgare*, archegonial projections of conical form, and in five out of the eight species the development of a cylindrical process, either as a direct continuation of the apex or from the under surface, resulted. Lastly, the not infrequent development of isolated members of the sporophyte may be referred to in this brief summary of results.

The sense in which the term apogamy has been used in the table above, requires a word of explanation. It seems inadvisable to restrict it to cases of the production of a sporophyte capable of continuing its growth as an independent plant. In the preceding pages, and in the remainder of this paper, the term apogamy is used to denote the vegetative production on the prothallus of a complete sporophyte or of

any member or groups of members of the latter; it may be further extended to include the production within the prothallus of tissue elements characteristic of the sporophyte. The common instance of the occurrence in the tissues of the sexual individual of a histological structure normally found only in the sporophyte is the presence of tracheides. The reasons for considering these elements a sufficient indication of apogamy will be considered below.

Reviewing in the first place the modifications which occurred in the form of the prothallus, it is seen that they appear in connection with the reproductive organs as well as in the continuation of ordinary growth. The mid-rib became well marked, and frequently very thick and dichotomous branching often occurred. As the apex of the prothallus continues to grow the thin lateral wings may fail to develop, and the prothallus assume the form of a cylindrical process, with little or no indication of dorsiventral structure, and terminate in a conical growing point. The same name has been applied to a similar growth from the under surface of the prothallus. This, in some cases at least, took the place, or was a further development of an archegonial projection. The latter structures often occurred in considerable numbers on a prothallus. Gametophytic budding sometimes occurred from archegonial projections, and the cylindrical process, when it arises in this position, may be regarded as a gametophytic bud of peculiar form. No reason is apparent why the cylindrical process, when it does not contain tracheides, should be considered as anything but a prothallus, the form of which has become modified under the influence of external conditions. The gametophytic nature of the process is confirmed by the presence of sexual organs and rhizoids upon it, by the occurrence of prothalloid outgrowths laterally from it, and by the readiness with which it re-assumes the flat prothalloid form and dorsiventral disposition of the sexual organs and rhizoids.

The ordinary type of gametophytic budding occurred in every culture and calls for no special notice except, perhaps, as to the situations in which the flat or filamentous prothalli develop. Besides arising from the margin, they were frequently present on a thickening of the apex; they also occurred on the under surface of the mid-ribs or the thin wing-like portions of the prothallus, and in some cases from archegonial projections. They were only rarely found to proceed from the necks of archegonia. In many cases, notably in the cultures of *Aspidium aculeatum* and *Athyrium niponicum*, GOEBEL'S* view that the gametophytic budding was due to "the weakening of the prothallus" by the influence of unfavourable conditions meets the facts. In such cases this was the common or almost exclusive form which the new growths assumed. In other cases, while gametophytic budding was common, the new growths from corresponding positions tended to assume the characters of the sporophyte. This was most common in well nourished prothalli.

While there is no reason to consider the cylindrical process as anything but a

* 'Sitz. d. k. Bayer. Akad. d. Wiss., vol. 26.

specially modified part of the prothallus, it must be recognised that the cylindrical form not only arises under dry conditions, but is that which analogy would suggest is better suited to these conditions. In view of this, the frequency with which tracheides occur in this portion of the prothallus acquires a special interest. A series of examples, leading from processes in which isolated tracheides or groups of tracheides occurred to those in which the process was traversed by a definite vascular strand occupying an axial position, was found. In the latter case, the structure of the strand justified its description as a rudimentary stele. Tracheides were also found, though less commonly, in the flat prothalloid regions of cylindrical processes, and in regions of the prothallus which showed no modification of external form. The presence of tracheides in archegonial projections, which is described by HEIM, was not observed in any of the prothalli examined. The structure of an archegonial projection with its distinction of a central group of cells from the external layers, the cells of which resembled those of the prothallus, certainly suggests a comparison with the cylindrical process; no direct relation between the central tissue of the projection and the vascular strand of a process could, however, be traced. The other common position for tracheides is the middle lobe. This was typically developed in *Nephrodium dilatatum* only, but from the frequent presence of sporangia upon it in that species, it acquires special interest. Its form and structure has already been described (fig. 40) and it only remains to consider its significance. In speaking of the middle lobe in *Pteris cretica*, DE BARY says: "The appearance of the middle lobe might be regarded as a very incomplete, persisting indication of budding, especially of the formation of the first leaf."* His figures also show that a leaf may develop in this position.† So far as the recognition of the sporophytic nature of the middle lobe is concerned, the observations on *Nephrodium dilatatum* support this. Further, in several other species, none of which, however, showed a typical middle lobe, a leaf or a leaf-like structure proceeded from the apical region. The evidence does not appear to me to be sufficient to justify the recognition of the middle lobe as in all cases a rudimentary leaf. When due regard is paid to the almost constant association of tracheides in the prothallus with undoubted cases of apogamy and their absence in the normal prothalli of all Vascular Cryptogams, the natural conclusion appears to be that the occurrence of these tissue elements may be considered as a simple case of apogamy.‡

A further assumption of sporophytic characters by the cylindrical process is seen in the presence of ramenta upon it, and the endogenous origin of roots in the tissue around a vascular strand may be considered as a phenomenon of the same nature. This view may at least be held until evidence connecting these isolated members with the imperfect development of a sporophyte is brought forward.

* 'Bot. Zeit.,' 1878, p. 464.

† *Ibid.*, fig. 16.

‡ This view differs from the opinion expressed in my Preliminary Statement, p. 257.

An interesting point in these preliminary attempts, as they may be called, to pass from a gametophytic to a sporophytic structure is the readiness with which the converse change takes place. The cylindrical process, even when it contains a vascular strand, readily assumes the flat prothalloid form. But, as the examples represented in figs. 64 and 65 show, even when in addition to the presence of a vascular strand, one or more ramenta have been formed on the surface, this change occurs. It would be possibly an undue use of terminology to call this change apospory. The fact that there is only a difference of degree between these cases and the production of prothalli on the first leaf of a sporophyte which has been developed apogamously may, however, be pointed out. This latter condition is known in a variety of *Nephrodium Filix-mas.**

The positions in which sporangia were found on prothalli of *Scolopendrium vulgare* and *Nephrodium dilatatum* have been fully enumerated. An examination of them leads to the conclusion that, apart from the fact that the portion of the prothallus on which the sporangia were situated contained tracheides and sometimes bore ramenta, it did not present evidence of being a reduced sporophyte. That the peculiarities of the tissue beneath sporangia are to be regarded as indicating the assumption of sporophytic characters, is indicated not only by the contrast between it and cells of the prothallus but also by the occasional association of sporangia with a vegetative bud. It need hardly be pointed out that this does not necessitate the assumption that the group of sporangia represents the result of reduction of a bud.† Even the occurrence of sporangia on the middle lobe in *Nephrodium dilatatum* is not, in the light of their occurrence elsewhere, sufficiently explained by regarding this region as a foliar structure. At least the early leaves of the young plants in this culture never showed any indication of the production of sporangia.

Turning to the production of normal buds the positions in which they occur form a series which helps to explain some of the intermediate structures discussed above. The first place may be given to those cases in which the bud is the result of further growth of a cylindrical process, the tip of which becomes sporophytic. The change is apparently always preceded by the formation of tracheides in a central position. The occurrence of a bud on the apex of the prothallus may be placed in connection with this. As the next step, the origin of buds from archegonial projections on the under side of the prothallus may be taken. This, which was well shown by *Doodia*,‡ is comparable to the development of the bud from the tip of a short cylindrical process, the intermediate stage between sporophyte and gametophyte being represented by the projection containing tracheides. From this the different prothalli in the same culture of *Nephrodium Filix-mas*, var. *polydactylum*, DADDS, lead to the direct production of the bud from the under surface of the prothallus.

* DRUERY. 'Linn. Soc. Journal,' vol. 29, p. 549.

† This was the view at first taken. 'Prelim. Statement,' p. 259.

‡ HEIM., *loc. cit.*

This series may be considered to be a natural one, not in the sense that the steps have been passed through to arrive at the condition of matters seen in *Pteris cretica*, for instance, but as placing the different cases of apogamy in a relation to one another, which admits of the corresponding parts being recognised. There is, in fact, a difference between them, depending on the more or less immediate assumption of sporophytic characters by the new growth.

From a slightly different point of view, a distinction can be drawn between two forms of apogamy. These may be termed induced apogamy and direct apogamy. As *induced apogamy*, all those cases may be classed in which the prothalli, under normal circumstances, become fertilised, but in which prolonged cultivation and other alterations in the conditions call forth a more or less complete assumption of the characters of the sporophyte by the prothallus or outgrowths from it. All the cases described in this paper, with the exception of a few of the varieties of *Nephrodium Filix-mas*, would come under this head. As *direct apogamy*, on the other hand, those cases may be grouped together, in which the prothallus at once produces a bud apogamously, no influence of external conditions being apparent. It remains to be seen, however, whether a modification of the external conditions will not induce these prothalli to return to sexual reproduction. All the three cases of apogamy described by DE BARY were of this sort.

There is another aspect of the apogamous growths from prothalli which may be briefly alluded to. Their occurrence depends upon the meristematic condition of the tissue of the prothallus, or of the capability of the latter to assume this condition. With this, the frequency with which growths occur from the apex may be connected, and to the capability of growth possessed by the cells around the ovum, which is usually called forth by fertilisation, the formation of archegonial projections may be ascribed. From these, either gametophytic budding or apogamy may take place. This association comes out in another way in *Polypodium vulgare*, where apogamy occurs in growths which begin as gametophytic buds, and many of which retain their prothalloid characters.

The conditions under which these cultures were made, was described in an early part of this paper. No endeavour was made to isolate the effect of the individual factors, but some general conclusions may be drawn, as to the relation existing between the results obtained and the nature of the conditions, which may suggest more accurate experimental work.

The series of cultures of *Nephrodium Filix-mas* shows that no necessary connection between cresting of the plant and apogamy exists. But though this statement is justified in view of the number of instances of apogamy now known in normal ferns, we are not in a position to decide that the fact, that nearly all the prothalli investigated were derived from crested plants, has been without influence on the results. It may be that prothalli of normal forms of these species will be found to behave similarly under like conditions. But it appears not improbable that

the variability of the fern plant, as indicated by the crested condition of its fronds, *predisposed* to the more or less ready occurrence of apogamy. Of the more direct causes two can be indicated. The prevention of fertilisation stands in somewhat the same relation to the occurrence of apogamy as "sporal arrest" has been shown to hold in certain cases of apospory.* Further, the influence of direct illumination on these shade loving organisms may be presumed to have had a considerable direct effect. This was the case specially with regard to the production of sporangia which ceased in cultures of *Scolopendrium vulgare* and *Nephrodium dilatatum* on their removal from the brightly illuminated green-house at Kew to a fern-case in a room at Glasgow. Further experiments are necessary to decide which factors are most important, and to ascertain whether exposure to such conditions will not induce apogamy in prothalli of most ferns.

These conditions suggest the possibility of similar changes taking place in nature. A large number of prothalli of *Nephrodium dilatatum* and a few of other species have been examined with this object, but so far without success. This negative evidence, however, rests on too small a basis to possess any value. The examination of prothalli found wild was of use, however, in showing how unlikely it is that conditions such as those found to induce apogamy would occur in a climate like that of the West of Scotland where the observations were made. The abundant moisture leads to the fertilisation of most of the prothalli before they had attained any considerable size. It is in districts with a suitable climate, especially with a well-marked dry season, that apogamy may be expected to occur. Records of the condition of large numbers of prothalli collected in the open are, however, wanting. That such conditions do exert a somewhat similar effect to that observed in cultivation at least upon the form and texture of the prothallus is suggested by the case of some species of *Gymnogramme*.† (*G. leptophylla*, *G. chærophylla*.) In these a fleshy conical outgrowth of considerable size arises from the under surface, in place of the cushion of ordinary polypodiaceous prothalli. This bears the archegonia, and have been termed a "Fruchtspross." This fleshy structure buries itself in the soil and enables the prothallus to exist between the periods of vegetative activity. In the case of *Gymnogramme leptophylla*, the relation which the development of this body bears to the seasons of the Mediterranean region and its biological significance have been pointed out by Goebel. It has been shown above that fleshy outgrowths in a similar position can be induced in prothalli which are usually of normal shape and texture by conditions somewhat similar to those to which the prothalli of *G. leptophylla* appear to have become definitely adapted. From the readiness with which such a change can be induced, it seems inadvisable to lay stress on a distinction of this kind for systematic purposes. This holds especially for the attempt which has been made to distinguish two main groups of Polypodiaceæ according to the flat

* Bower, 'Linn. Soc. Trans.,' 1887, p. 312.

† Goebel, 'Bot. Zeit.,' 1877. 'Flora,' 1889.

or tuberous nature of the gametophyte. This difference is rather comparable to such an adaptive character as the succulence of some xerophytes, and the origin of the definite adaptation in some species of *Gymnogramme* may be looked for with probability in the capacity which other fern prothalli show of reacting to dry conditions in a similar way.

The Bearing of Apogamy on the Origin of Alternation of Generations in Archegoniate Plants.

It was stated at the commencement that facts of the kind described and discussed above derive their chief interest from their possible bearing on the nature of alternation of generations in the Archegoniatæ. This will now be considered. Although it is not the purpose of this paper to enter into a full discussion of the problem of alternation, it is impossible to avoid its general consideration in any attempt to estimate the weight to be attached to the evidence afforded by deviations from the normal life-history, such as the phenomena of apogamy and apospory. The different assumptions which have been made in discussing the question necessitate this: the general problem will however be dealt with only so far as to define the author's position on some points on which a clear understanding is necessary, although in the present state of our knowledge they must be regarded as working assumptions merely. The views entertained with regard to some of these questions profoundly affect the value to be attached to some phenomena, among which those discussed in this paper are included. It may be as well to state at the outset that only the facts of alternation seen in Archegoniates and some of the Green Algæ will be considered. The gain in clearness justifies the limitation of comparisons to organisms, some of which may be presumed to represent more or less accurately steps through which the ancestors of Bryophyta and Pteridophyta may have passed.

The nature of the problem may be thus stated. The sexual generation of the Bryophyta and Pteridophyta may reasonably be assumed to have been derived by direct descent, with modification, from algal forms, something like those presented by the *Œdogonium* or *Coleochæte* thallus* at the present day. Two main views of the origin of the sporophyte are however possible.

(1.) That the sporophyte is also to be traced back to, originally, independent individuals, similar to those from which the gametophyte arose, *i.e.*, to forms represented by the asexual individuals in the life-history of *Œdogonium*; the almost invariable alternation, and the permanent or temporary dependence of the sporophyte on the sexual generation, are subsequent adaptations. On this view the two generations of an archegoniate plant would be comparable with two individuals of, *e.g.*, *Œdogonium*, the one reproducing sexually, the other asexually. This is homologous alternation.

* It is hardly necessary to point out that these and other references to existing Algæ are mere illustrations, and are not meant to imply that any living Alga is closely allied to the ancestral forms, from which the Archegoniatæ were derived.

(2.) That the sporophyte is not to be traced back to free living individuals of the ancestral algal form, but has a distinct phylogenetic history, having nothing in common with the asexual *Œdogonium* plant in the above hypothetical illustration, save that the ovum is the starting point in its development. In this sense the sporophyte is an interpolated stage in the life-history, the mode of origin of which is illustrated by the result of germination of the zygote in such a series of living forms as *Œdogonium, Coleochæte, Riccia, Anthoceros.* From a complex sporophyte like the last the simplest sporophytes of the Vascular Cryptogams are supposed to have been derived. On this view the two generations of an archegoniate are not comparable with two individuals of, *e.g.*, *Œdogonium*, but with a sexual individual the fertilised ovum of which developed in connection with the parent into what was at first a fruit, but in later evolved forms became an independent organism, though it always remained for a time dependent on the sexual plant. The alternation is on this view antithetic.

The essential distinction between the two views lies in this, that on the former the second generation, however reduced, is to be traced back to free living individuals, while on the latter the second generation never consisted of independent forms like the sexual plant. The above is a brief statement of the two alternative theories of the nature of alternation in the archegoniates which have been treated of fully by PRINGSHEIM and SCOTT, and by CELAKOVSKY, VAIZEY, and BOWER.

In the absence of any direct evidence as to the nature of the causes which led to the origin of a definite alternation of generations, it is necessary to have recourse to hypothesis. This has been successfully done by BOWER,* and a consistent theory of how the spore-bearing generation might have been derived by elaboration of the zygote has been framed by him. The fundamental idea of this theory, that the second generation in archegoniates is an adaptation to a terrestrial life, and that its origin was associated with the spread of algal forms to the land, must form the starting point of any hypothesis. It holds even if the view that the two generations are homologous, and were originally similar, is adopted. In the works of Professor BOWER a full discussion of the theory of antithetic alternation will be found. That the methods of advance there indicated were probable ones, if the line of evolution followed is really indicated by the series of Bryophyte sporogonia and the simplest Pteridophyta, appears to be a sound conclusion. In the first of the 'Studies in the Morphology of Spore-producing Members,' Professor BOWER assumes that the sporophyte of the Vascular Cryptogams was derived "from some simpler form more or less like that of the lower Bryophyta." The explanation which follows of the mode of increase in complexity of the sporogonium in the Bryophyta appears to be highly probable, and the suggested changes which might have led to the development of the "simpler vascular plants with foliar appendages and discrete archesporia from forms with no appendicular organs and an undivided and concrete archesporium" are

* 'Annals of Botany,' 1890 and 1894; 'Phil. Trans.,' 1894.

doubtless quite possible ones. But the question remains whether the gap between the Bryophyta and the Vascular Cryptogams is not an essentially natural one, and not simply due to our ignorance of intermediate forms. The possibility of the origin of the Archegoniatæ being polyphyletic has been clearly indicated by BRAUN,* and GOEBEL's words† seem to imply a similar view. Certainty on this point is impossible, but there appears to be no reason to prevent our regarding Bryophytes and Pteridophytes as independent derivations of the primitive algal stock, and further admitting the possibility that the separate groups of these two great divisions may also have had independent though parallel lines of descent. This possibility becomes almost a probability when the origin of the second generation is related to the spread of primitive algal forms to the land. For it may be regarded as more likely that a number of the latter would become modified in a similar way under similar conditions than that all existing groups of archegoniate plants are to be traced back to a single point of origin from the algal ancestry, their divergent lines of descent from which are indicated by some of the existing forms of life.‡ The possibility of the independent origin of the Bryophyta and Pteridophyta has been one of the reasons which led me to consider in the light of experiments upon fern prothalli how far it is possible to frame an alternative hypothesis of how the two generations could have arisen, and assumed their definite relation to one another, if they did not arise in the way supposed by the antithetic theory. For it follows from the possibility of the polyphyletic origin of the vascular plants that such a group as the Ferns, which we have as yet no positive evidence to derive from any of the other groups, may be considered to some extent by themselves. This consideration appears to me to lessen the force of the objection, which has been raised to the use of the phenomena of apogamy and apospory for phylogenetic purposes, that they are as yet unknown in such groups as the Lycopodineæ.§

The Ferns appear in some respects the best suited of the Vascular Cryptogams for the attempt to obtain experimental evidence on the nature of alternation of generations. If the gametophyte and the sporophyte are to be traced back to originally similar stages of a primitive organism, it is evident that the sexual plant has diverged less widely from the latter than the sporophyte has. Among the Vascular Cryptogams

* "The mosses are to be regarded as a further, and, in fact, as it appears, geologically late development from the Thallophytes." 'Monatsber. d. k. Akad. Wiss., Berlin.' 1875, p. 245, note. The philosophical considerations on the nature of alternation in plants, and the clear recognition of the important bearing on morphological questions of the polyphyletic origin of the higher forms, are in many points still unrecognised in current views on homology.

† "One will have to look for the point of attachment of the Pteridophytes elsewhere than among the Muscineæ, in forms which may have been similar to Liverworts, but whose asexual generation has from the first proceeded on another line of development." SCHENK's 'Handbuch,' vol. 2, p. 401.

‡ This is the logical outcome of the view that the Archegoniates have had a monophyletic origin. It is indicated in many diagrams of the affinities of the various groups.

§ BOWER, on "Apospory," 'Trans. Linn. Soc.,' 1887, p. 323.

the Ferns possess the least specialised form of gametophyte, in their independent prothallus, capable of assimilation, and agreeing in its general form with the simplest gametophytes of the Bryophyta. It is not an unreasonable hope that with this simple form and structure the fern prothallus may have retained some of the physiological properties of the primitive organism. In particular the irritability owing to which external stimuli called forth the variations which led to the evolution of the sporophyte may still exist. Under somewhat similar conditions changes may be induced the nature of which may afford hints of the sort of variations to be used in picturing the original course of evolution.

The results which have been described appear to justify the method. The changes which occurred in the prothalli are not regarded as reversions. The prothallus, by preventing its fertilisation, and by exposure to direct illumination, has been exposed to conditions which, on Professor BOWER'S hypothesis, conduced to the evolution of the sporophyte. No reason is apparent why, if the antithetic theory is correct, these conditions should induce any change in the gametophyte which would lead it to assume the characters of the sporophyte more or less completely. But, on the view that it was under such conditions that the sporophyte was evolved from individuals resembling the gametophyte, those results are less surprising. It has been seen that any member of the sporophyte may arise on the gametophyte, and the tissues of the latter may undergo differentiations which are usually found only in the fern plant. It may be objected that the members produced on the prothallus, with the possible exception of some of the rudimentary sporangia, exhibited no indication of primitive structure. While this is true, it might almost have been anticipated when the nature of the experiment is considered. These organs have become evolved and specialised on the sporophyte, and when the gametophyte is exposed to conditions which cause it to assume the characters of the latter, the perfected structures are produced.

Having pointed out the light in which the phenomena of induced apogamy may be regarded, the changes by which two homologous generations, associated as we see them in the ferns, *might* have been evolved will be indicated for the sake of comparison with the antithetic theory. The life-history of some of the algal forms which spread to the land would of course remain unchanged, the organisms passing the dry periods in a dormant condition, as is the case with some algæ at the present day. In others, which became more thoroughly terrestrial, a change from the filamentous to the flattened form might take place; this, in part, might result from the influence of light, but the advantage of a close contact with the soil must also be taken into account. The archegonium in its various forms may be looked upon as an adaptation of the female sexual organ to such conditions. The flattened organism, resembling a fern prothallus or a simple liverwort in form, would still represent the gametophyte only, though asexual modes of reproduction may have been present. Exposed, however, to conditions which rendered the opportunities for zoidiogamic fertilisation infrequent, the organism in the intermediate dry periods might assume a form

(possibly as a direct result of the external conditions) better suited to endure drought. This we may picture as resembling a cylindrical process. If at the same time these modified organisms became capable of producing reproductive cells capable of dispersal in the dry state, a primitive sporophyte would be in existence. The reproductive cells (spores) of this form would on germination produce organisms capable of sexual reproduction, but which under dry conditions would grow into the spore-producing form. This explanation so far does not account for the connection of the sporophyte with the gametophyte. If, however, after a short wet period, in which fertilisation had been effected, a dry period ensued, and the ovum, instead of forming swarm spores, germinated *in situ*, the first step in this direction would have been taken. This organism, under the dry conditions acting from the first, would soon assume the characters of the sporophytic form and be capable of multiplication by means of dry spores. A transient sexual stage would probably in the first instance precede this, however. The result of germination of the spore, since this could only take place in a damp spot, would invariably be the sexual form. The inconstent character of the alternation, due to the capability of any sexual individual to assume the asexual form under dry conditions, would be lost, as the sporophyte increased in complexity. The development of absorbent organs (roots) ensuring a supply of moisture under the dry conditions, associated with the start given to the individual arising from the fertilised ovum by its connection with the parent sexual plant, may be supposed to have been some of the factors in the elaboration. Further, the fact that division of the zygote into swarm spores had not occurred may even at this early stage have been associated with a difference in constitution of the cells of the primitive sporophyte. As divergence of the characters of the two forms, the sexual and the asexual, continued, the latter would form a vegetation capable of shading the soil and keeping it moist. The conditions necessary for the development of the spores into the sexual form and the ready fertilisation of the latter would be ensured, and the prothallus would persist as a stage in the life-history. Any tendency to increase in complexity would be checked by the fact that fertilisation and the development of the sporophyte would bring about the death of the gametophyte. As the two generations continued to diverge from one another, the early stage of the sporophyte in which it resembled the gametophyte would become reduced, and ultimately disappear.

The above hypothesis may prove to be of use in showing that it is possible to form a connected view of how a regular alternation of generations, such as that seen in Ferns, may have arisen by the differentiation of two primitively similar (homologous) individuals, the one into the sexual the other into the asexual form. It is, of course, possible that, so far as the difference in mode of reproduction was concerned, the two forms may have already existed, though not in necessary connection with one another, in the life-history of the algal ancestor. The hypothesis has been stated without reference to this, because the behaviour of fern prothalli in which apogamy is induced affords examples of almost every step assumed by the theory. Thus the assumption

of the flattened form, the further growth and change in form and structure of unfertilised prothalli, the production of sporangia, the acquisition of roots by the fleshy cylindrical process, and lastly the direct continuation of such a process into a normal stem bearing leaves, were all found in *Scolopendrium vulgare*. The association of the two forms, *i.e.*, the growth of a prothallus, capable of assuming the cylindrical form and producing sporangia, from the zygote, has never been seen, and it would be, perhaps, too much to expect that further experiments may produce it.

It cannot be too strongly insisted upon that the above is put forward merely as a *provisional hypothesis* which serves to connect together a group of facts, the further study of which must modify, and will possibly disprove it. It may, however, be used as the basis of a comparison with the antithetic theory to ascertain which facts are best explained by the one and which follow most naturally from the other theoretical view. This will be done under the following heads :—

(1.) Alternation in Bryophyta and some Algæ.
(2.) Normal life-history of Pteridophyta.
(3.) Abnormal modes of reproduction in Bryophyta and Pteridophyta.
(4.) Cytological distinctions between the sexual and asexual generations.

(1.) *Alternation in Bryophyta and some Algæ.*

These groups agree in that the second generation appears as a group of spores or as a more or less complex fruit. They may be conveniently referred to together without implying a necessary genetic connection between the forms compared. It is in its application to the series of the Bryophyta that the theory of antithetic alternation is seen to connect the facts in the most natural manner. I have nothing to add to the suggestions made by PRINGSHEIM and SCOTT as to the possible explanation of the origin of the Bryophyte sporogonium on the hypothesis of homologous alternation. In this case, however, it appears to be possible to regard the mode of increase in complexity of the sporogonium as independent of the question whether the alternation is homologous or antithetic. If the group of cells resulting from the division of the zygote in *Œdogonium* or *Coleochæte* be regarded as representing the structure from which the evolution of the sporogonium (which remains throughout dependent on the parent plant) started, it is clear that this starting point was a group of spore-producing cells. Whether this was the result of simple elaboration of the zygote, or represented a reduced first neutral generation, is of theoretical importance, but need not affect our views of its further course of development, and the methods of advance. This on either view may have taken place by such steps as those indicated by BOWER, sterilisation of potentially spore-producing cells playing an important part. If this view of the history of the sporogonium is correct, and the evidence for it derived from comparison of plants probably genetically connected with one another appears to be strong, it is probable that experiments would fail to induce apogamy in this group.

This opinion is not inconsistent with the occurrence of apospory in Mosses, which will be considered later.

(2.) *The Normal Life-Histories of Pteridophyta.*

These afford little evidence in support of one or the other theory of the nature of alternation. On the homologous theory some rudiment of the sexual stage might be looked for during the development of the sporophyte. The facts of ontogeny mostly afford merely negative evidence, though the "Analogy between the young asexual generation and the sexual generation"* in *Lycopodium cernuum* pointed out by TREUB, may be explained in this way.

(3.) *Abnormal Modes of Reproduction in Pteridophyta and Bryophyta.*

Apogamy and apospory are the most important phenomena which come under this head. The former is known only in Leptosporangiate Ferns, the latter in the Mosses as well. Though conveniently considered together it does not follow that the evidential weight to be attached to them is equal. Both are commonly regarded as indicating that the distinction between the two generations is not a rigid one. Beyond this, which is indeed nothing more than a statement of the facts, widely divergent opinions have been expressed. The explanation which may be given on the theory of homologous alternation may be first considered, since the views held by authors who have written from the standpoint of the antithetic theory are rather critical than constructive.

It is unnecessary to add anything further regarding the possible significance of the facts of induced *apogamy*, with which instances of direct apogamy have been connected by intermediate forms, on the theory of homologous alternation. On the view that the sporophyte is descended from a similar form to the gametophyte, a comparison of *apospory* with gametophytic budding suggests itself. The position of the aposporous growths may similarly be related to the capacity of the cells of the part for further growth. From this point of view the cases of apospory, in which prothalli spring from the first leaves of the sporophyte, are of special interest, while they are those least easily accounted for on any other theory. The existence of cases of induced apospory in Mosses is important in that it shows that this deviation from the normal is not confined to one group of plants. By many they are regarded as affording strong evidence of the homology of the two generations. In view of a possible explanation which would be satisfactory, whichever theory is correct, it seems inadvisable to lay stress upon this phenomenon. This will be referred to in the next section.

The possibility of accounting for apogamy and apospory on the hypothesis of antithetic alternation must be dealt with more fully, since, at first sight at least,

* 'Am. d. Jard. Bot. de Buitenzorg,' vol. 4, p. 135.

they appear to be "facts which ought not to happen" if that theory is correct. Apospory, as will be shown, presents no special difficulty. With apogamy the case is different, and, so far as I am aware, no satisfactory explanation has been given. Any explanation must take into account not merely the production of a sporophyte in the position which a normal embryo occupies, but the occurrence of ramenta, sporangia, &c., on regions of the prothallus, which in form and structure appear to be intermediate between gametophyte and sporophyte. Apart from the cytological bearings of the subject the most suggestive view of a possible explanation on the lines of the antithetic theory is that the capabilities of development of the succeeding generation must be present in the intermediate one in order to appear in its reproductive cells.* Whether the not infrequent association of apogamy with the sexual organs has any significance in this relation must be considered in attempts to arrive at the true explanation of the phenomenon. In the present state of our knowledge a fuller discussion of these questions would be useless.

There are two points, however, which affect the value of the evidence afforded by apogamy and apospory in phylogenetic inquiries, which must be referred to. The view which has been expressed by Professor BOWER, "that these are phenomena of a teratological nature, and are not to be taken as evidence with regard to the evolutionary relations of the sporophyte and gametophyte,"† may doubtless be applied to the results of prolonged cultivation exhibited by some of the prothalli described in this paper. It may be remarked, however, that any criterion by which to decide when variations pass into monstrosities is wanting. This is especially the case with "discontinuous variations." This being so the usefulness of any particular class of variations in phylogenetic study must be decided on its own merits. Reasons have been indicated in the previous pages why the variations of fern prothalli, which are in many instances gradual and slight, and apparently beneficial under the conditions of life, are entitled to some degree of weight for such purposes. Under these circumstances it appears to be of little importance whether they are termed variations or monstrosities.

In connection with this, it may be pointed out that another of the reasons which led Dr. BOWER to regard these phenomena as of secondary importance has been considerably modified by the subsequent progress of investigation. In the sentences preceding the one above quoted, he points out that "both apogamy and apospory are decidedly rare phenomena; that they appear for the most part in plants of variable species and under conditions of cultivation which are not those natural to the plants. Moreover, attempts to induce apospory, though successful in certain Mosses, have been entirely without result in Ferns." Since this was written, a number of additions to the list of Ferns which exhibit apogamy have been made; I would venture to suggest that under conditions such as those of the present series of

* This suggestion I owe to Professor FARMER.

† 'Annals of Botany,' 1890, p. 368.

experiments, their number might be rapidly increased. As this is a point of considerable importance, I subjoin a list of ferns which are known to be apogamous. In the case of those to the names of which an asterisk is prefixed, this deviation is only known in crested or otherwise abnormal forms.

Osmundaceæ.	Hymenophyllaceæ.	Polypodiaceæ.
Todea Africana	Trichomanes alatum	Ceratopteris thalechoides
T. rivularis		Pteris cretica
T. pellucida		Nephrodium Filix-mas
Osmunda regalis		,, falcatum
		* ,, dilatatum.
		* ,, Oreopteris
		Aspidium aculeatum
		* ,, angulare
		,, frondosum
		Doodya caudata
		*Scolopendrium vulgare
		Notochlaena distans
		*Athyrium Filix-fœmina
		,, niponicum

When it is remembered how few the definite attempts to induce the phenomenon have been, the list is not an inconsiderable one.

The species in which apospory has been recorded may be tabulated for the sake of comparison. It is noteworthy that the majority of these Ferns are known to be apogamous.

Hymenophyllaceæ.	Polypodiaceæ.
Trichomanes alatum	Athyrium Filix-fœmina
,, Kaulfussii	Aspidium angulare
,, pyxidiferum	Scolopendrium vulgare
	Nephrodium Filix-mas
	Onoclea sensibilis
	Pteris aquilina

(4.) *Cytological Differences between the Sporophyte and Gametophyte.*

It has been shown in recent years that accompanying the more obvious distinctions between the two generations a difference in their nuclei could be detected during karyokinesis. In the examples of Bryophyta, Pteridophyta, Gymnosperms, and Angiosperms which have been investigated, the number of chromosomes was twice as large in the nuclei of the sporophyte as on those of the corresponding gametophyte. The facts are collected in a paper by STRASBURGER,* and their bearing on alternation

* 'Annals of Botany,' 1894.

has been considered by BOWER* and SCOTT†, among others. It is, therefore, only necessary to consider in what degree they lend support to the theories of antithetic or homologous alternation. The relation of the nuclear differences to normal alternation are in such natural accord with the view that the sporophyte is an interpolated stage in the life-history, that STRASBURGER was led on these grounds to adopt a theory of alternation, essentially the same as that previously arrived at by BOWER, by comparison of development and structure.

As to the nuclear changes which take place in apospory and apogamy, no facts have yet been ascertained. The only aspect of the question which can be considered is how far these departures from the normal are inconsistent with the assumption of the fundamental importance of the nuclear distinction between the two generations.

Apospory presents no special difficulty on either theory. For a reduction in the number of chromosomes, which is known to take place in the spore mother cells, may be supposed to take place in vegetative cells. As in the former case this is associated with the capacity of the cells with the half number of chromosomes to develop into the gametophyte, so in the latter case the same result would presumably follow. The cells being still in continuity with the tissues of the sporophyte, their further growth results in the aposporous development of a prothallus. It is more difficult, however, to see in which manner apogamy can be dependent on a nuclear change. The sharp contrast between the sporophytic tissue and that of the prothallus, which has been mentioned several times in the preceding pages, is in favour of some such change occurring. The result may possibly be associated with a nuclear fusion, and it has been shown that not infrequently two nuclei occur in the cells of *Scolopendrium* near the boundary line between sporophytic and gametophytic tissue. But it may be pointed out that, whatever the change may be, it can occur independently of the sexual fusion, which occurs in fertilisation. This implies a modification of any view of the necessary association of the origin of the second generation with the result of fertilisation. The correlation of the double number of chromosomes with the sporophyte might, in the light of the facts of induced apogamy, be regarded as due to a subsequent association, and not as the fundamental fact in the origin of the neutral generation. All speculation on these points must, however, be tentative until the actual condition of matters in apogamy and apospory has been ascertained.

CONCLUSION.

In this paper the possible value of the study of apogamy in Ferns as one of the lines of evidence which bear on the nature of alternation in archegoniate plants has been considered. This has been done on the basis of results obtained from a series of

* 'Trans. Bot. Soc. Edinb.,' 1894.
† *Loc. cit.*

experimental cultures, and the nature of the facts necessitated special prominence being given to the hypothesis of homologous alternation. The attempt has been made to suggest some of the steps by which such a group as the Ferns might have originated on that hypothesis. It appears advisable in order to guard against possible misconception to state that in the author's opinion no preponderating evidence in favour of either theory and no facts rendering one or the other untenable are known. Both the theories of antithetic and homologous alternation afford possible explanations of the facts of the normal and abnormal life-history of such a group as the Ferns. The reasons which make one or the other appear more probable, depend on the assumptions made as to the line of descent which has been followed, and the degree to which the groups of plants now living have had a common origin and represent actual steps in the process. Under these circumstances it is necessary to regard the question as an open one until the available sources of evidence, some of which have been indicated, have been more fully investigated. As one of the methods which may be expected to yield interesting results, the extension of cultural experiments under accurately known conditions to the Archegoniatæ, a method which has proved of great value in the study of the life-histories of Thallophyta, may be specially mentioned.

The first part of this investigation was conducted in the Jodrell Laboratory of the Royal Gardens, Kew, and it has been continued in the Botanical Laboratory of Glasgow University. I have thus had the advantage of the advice and help of Dr. Scott and Professor Bower, to whom I wish to express my special indebtedness. My thanks are also due to Professor Farmer and Mr. D. T. Gwynne-Vaughan for helpful criticisms and suggestions, to Dr. Chree for the statement on the weather of 1896, to Mr. Druery for the supply of some of the material, and to the authorities of the Royal Gardens, who gave me every facility for carrying on the cultures. To the kindness of Dr. W. B. Brodie I owe the photograph from which fig. 69 has been made.

Description of Figures.

(*Note.*—Where not otherwise stated, the figures represent prothalli magnified between six and seven diameters.)

PLATE 7.

Scolopendrium vulgare.

Fig. 1. Prothallus from above, showing a cylindrical process developed from the apex.

Fig. 2. Prothallus from the side, showing a cylindrical process developed from the under surface. $x =$ anterior margin.

Fig. 3. Transverse section of a thin cylindrical process. (× 70.)

Fig. 4. Cylindrical process re-assuming the prothalloid form.

Fig. 5. Prothallus with cylindrical process, the tip of which shows the first indication of developing into a sporophyte.

Fig. 6. Longitudinal median section of the tip of fig. 5, along the dotted line. The sporophytic tissue is shaded; the group of cells isolated in the figure was in connection with the main mass. (× 100.)

Fig. 7. Longitudinal section of a slightly older but similar bud; the sporophytic tissue is shaded. (× 25.)

Fig. 8. Prothallus of the variety *marginale*, showing a bud developed on a projection from the under surface.

Fig. 9. Terminal portion of a prothallus, on the under surface of which to the right is a prothalloid growth, and to the left a similar structure, which has continued as a simple leaf bearing ramenta. (× 25.)

Fig. 10. Prothallus from the branched cylindrical process of which ten roots arose; eight of these are visible.

Fig. 11. Prothallus of the variety *marginale*; a single root arises from the process on which archegonia are present.

Fig. 12. Longitudinal section of a cylindrical process, showing a young root still enclosed in the tissue. In the axial vascular strand, tracheides, the position of which is indicated by the dark shading, are present. (× 25.)

Fig. 13. Similar section of a part of the process in fig. 10, showing the insertion of an older root. (× 25.)

Fig. 14. Transverse section of the axial vascular strand in one of the branches of the process of fig. 10. T = tracheides. S = sheathing layer of cells. (× 300.)

Fig. 15. Prothallus with a thick flat process seen from above. *sp.* = sporangia. ♀ = archegonia.

PLATE 8.

Scolopendrium vulgare.

Fig. 16. Prothallus with archegonial projections on the under surface, and on the massive cylindrical process two groups of sporangia; one of these groups is accompanied by two ramenta. (× 25.)

Fig. 17. Longitudinal section of a cylindrical process showing a group of well-developed sporangia on an archegonial projection in which tracheides, indicated by the dark shading, are present. (× 12.)

Fig. 18. Cylindrical process bearing sporangia on its tip along with a vegetative bud. *a.* = archegonia; *sp.* = sporangia. (× 25.)

Fig. 19. Longitudinal section of an imperfect sporangium. (× 170.)

Fig. 20. Normal sporangia in two stages of development: in *b*, the sporogenous group and the two layers of tapetum have become developed. (× 170.)

Fig. 21. Group of sporangia (sp.) from the prothallus in fig. 15, to show the contrast between the underlying tissue and that of the prothallus. In some of the cells of the sub-sporangial tissue two nuclei are present. (× 170.)

Fig. 22. Group of sporangia (sp.) on a projection, the structure of which indicates its relation to an archegonium. (× 600.)

Fig. 23. Group of tracheides developed beneath an archegonium neck. In some of these and in cells of the adjoining tissue two nuclei are present. (× 300).

Fig. 24. Longitudinal section of the process and bud in fig. 18. The vascular strand is shaded, the position of tracheides in it being indicated. *ar.* = archegonia; *x.* = level of attachment of the lowest sporangium. (× 25.)

Nephrodium dilatatum.

Fig. 25. Small prothallus with a well-developed middle lobe, viewed from the under surface. On the cushion are a number of archegonial projections.

Fig. 26. Prothallus with middle lobe bearing a rudimentary sporangium. Growth has taken place from the margin to one side of this.

Fig. 27. Prothallus, the middle lobe of which bears an imperfect sporangium of considerable size. Growth has taken place from the anterior margin on both sides of the apex.

PLATE 9.

Nephrodium dilatatum.

Fig. 28. Prothallus from the side; the middle lobe bears a sporangium. On the under surface are small archegonial projections and behind the apex a cylindrical process which soon becomes flat and prothalloid.

Fig. 29. Prothallus from the side; a row of sporangia occupy the anterior margin and others are situated on the upper side of the cylindrical process.

Fig. 30. Prothallus from upper side; the middle lobe bears a perfect and almost mature sporangium: the process has retained its cylindrical form.

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Fig. 32. Prothallus from below; the apex continued directly as the cylindrical process: from behind the tip of this a similar process has arisen.

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Fig. 35. Apex of prothallus on which a number of sporangia are situated. The one which corresponds to the apex of the middle lobe is more massive than the rest. The cylindrical process is still short. (× 25.)

Fig. 36. Cylindrical process from the under side of which a small branch of similar form arises; behind this a group of almost mature sporangia is situated among the rhizoids.

Fig. 37. Apex of a cylindrical process bearing ramenta; enclosed within these were young sporangia. (× 35.)

Fig. 38. Cylindrical process arising by the side of an imperfect sporangium (sp.); it bears a somewhat similar sporangium on the other side (sp.′), and on the tip are a number of sporangia associated with ramenta. (× 35.)

Fig. 39. Bud-like group of ramenta situated just behind the middle lobe which bears a sporangium. Tracheides were present in the thin continuation of the prothallus at *t*. (× 25.)

Fig. 40. Middle lobe from prothallus in fig. 25. (× 100.)

Fig. 41. Portion of the prothallus in fig. 42, including the middle lobe, *b*, and the strand of tracheides running from thence to an archegonium. (× 100.)

Fig. 42. Prothallus illustrating the nature of the cylindrical process, description in text. *a*, *b*, *c* = successively formed middle lobes; the last represented by a sporangium.

Fig. 43. Vertical section of an archegonial projection from a cylindrical process. (× 100.)

PLATE 10.

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Fig. 44. Vertical section of a rudimentary cylindrical process just behind the apex. (× 100.)

Fig. 45. An unopened archegonium, the cells of the neck of which have taken on further growth at *a*. (× 100.)

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Fig. 47. Vertical section of an archegonium, situated on a projection of the prothallus; in the canal of the neck two small tracheides have developed. (× 100.)

Fig. 48. Group of eight well-developed sporangia upon the base of a cylindrical

process. The middle lobe, which is seen to the right, bears an imperfectly developed sporangium. (× 100.)

Fig. 49. *a.* Group of spores from an almost mature sporangium on the prothallus.
b. Ripe spore from a sporangium developed on the sporophyte. (× 300.)

Fig. 50. Group of spores in section from a sporangium developed on the prothallus, (× 300.)

Fig. 51. Young sporangium from the tip of a cylindrical process. (× 300.)

Fig. 52. Imperfect sporangium from fig. 27; the shading at *t* indicates the position of a group of tracheides. (× 100.)

Fig. 53. Longitudinal section through the middle lobe and cylindrical process of a prothallus. Beneath the former, which bore sporangia (sp.), tracheides were present; their position is indicated by the dark shading. (× 25.)

Fig. 54. Similar section to fig. 53; in the strand of elongated cells beneath the single sporangium (*Sp.*) tracheides were not present. (× 25.)

Fig. 55. Longitudinal section through the tip of the process in fig. 38. Tracheides are present underlying the sporangia and ramenta. (× 100.)

Nephrodium Oreopteris.

Fig. 56. Prothallus with a single ramentum (*r.*) on the cylindrical process.

Fig. 57. Prothallus, the apex of which continues as a similar process to fig. 56; the two lobes on this agree with the ramenta in form and position but their cells resembled those of the prothallus.

Aspidium aculeatum.

Fig. 58. Old prothallus of a uniform brown colour, from the under side of which gametophytic budding has taken place in connection with archegonial projections. One of the growths resembles a cylindrical process at its origin.

Fig. 59. Similar prothallus bearing an apogamously-produced sporophyte; the six leaves of the latter are of similar simple form.

Aspidium angulare.

Fig. 60. Apical region of a prothallus seen from the under side; it bears an archegonial projection and two young buds, one of which arises from the margin. (× 25.)

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Fig. 61. Abnormal archegonium, the ovum of which has undergone division. ($\times$ 170.)

Fig. 62. Tip of a prothallus from below. It bears a ramentum and an apogamously-produced bud. ($\times$ 25.)

Fig. 63. Prothallus with a ramentum on each side of a flat continuation of the apex which bears a bud. ($\times$ 25.)

Fig. 64. Growth bearing ramenta which arises in the position of a bud; its further growth is prothalloid. ($\times$ 25.)

Fig. 65. Growth with the characters of a leaf-stalk which has resumed the prothalloid form. t = tracheide.

Athyrium niponicum.

Fig. 66. Prothallus, with numerous archegonial projections; some of these continue as processes which soon become prothalloid; tracheides were present in the stalk-like region.

Fig. 67. Prothallus, the apex of which has continued as a cylindrical process; an archegonial projection arisës from the under surface.

A. niponicum var. *cristatum.*

Fig. 68. Similar prothallus to fig. 66, but no tracheides were present in the gametophytic bud.

Aspidium frondosum.

Fig. 69. Photograph of a prothallus which bore six buds on the anterior margin. Two of these are seen to the left. ($\times \frac{3}{4}$.)

Athyrium Filix-fœmina.

Fig. 70. Prothallus which bears an apogamously-produced sporophyte on the apex: on the under surface, further back, is seen a normal embryo arrested at an early stage.

Fig. 71. Bud situated on the tip of a thick narrow continuation of the prothallus apex, which contains tracheides.

Fig. 72. Cylindrical process from the under surface of a prothallus: this continues into the leaf-stalk with no indication of a stem apex.

Fig. 73. Longitudinal section of a cylindrical process in which two groups of tracheides (t) are seen; near the tip is an embryo, apparently endogenous. (× 25.)

Polypodium vulgare.

Fig. 74. Prothallus producing a bud from its apex.

Fig. 75. Two apogamously-produced buds on a portion of a prothallus, one arises from the margin, the other from one of the filamentous prothalloid growths which are seen just within the margin. (× 25.)

Fig. 76. Prothalloid growth, which has continued into a narrow leaf-like lobe: in the shaded region of this, intercellular spaces were present.

Nephrodium Filix-mas.

Fig. 77. Prothallus of *Nephrodium Filix-mas*, which continues as a thick almost cylindrical structure. The small cylindrical process which springs from the under surface bore a ramentum and contained tracheides.

Fig. 78. Anterior end of prothallus of the same variety; it bears archegonial projections. (× 25.)

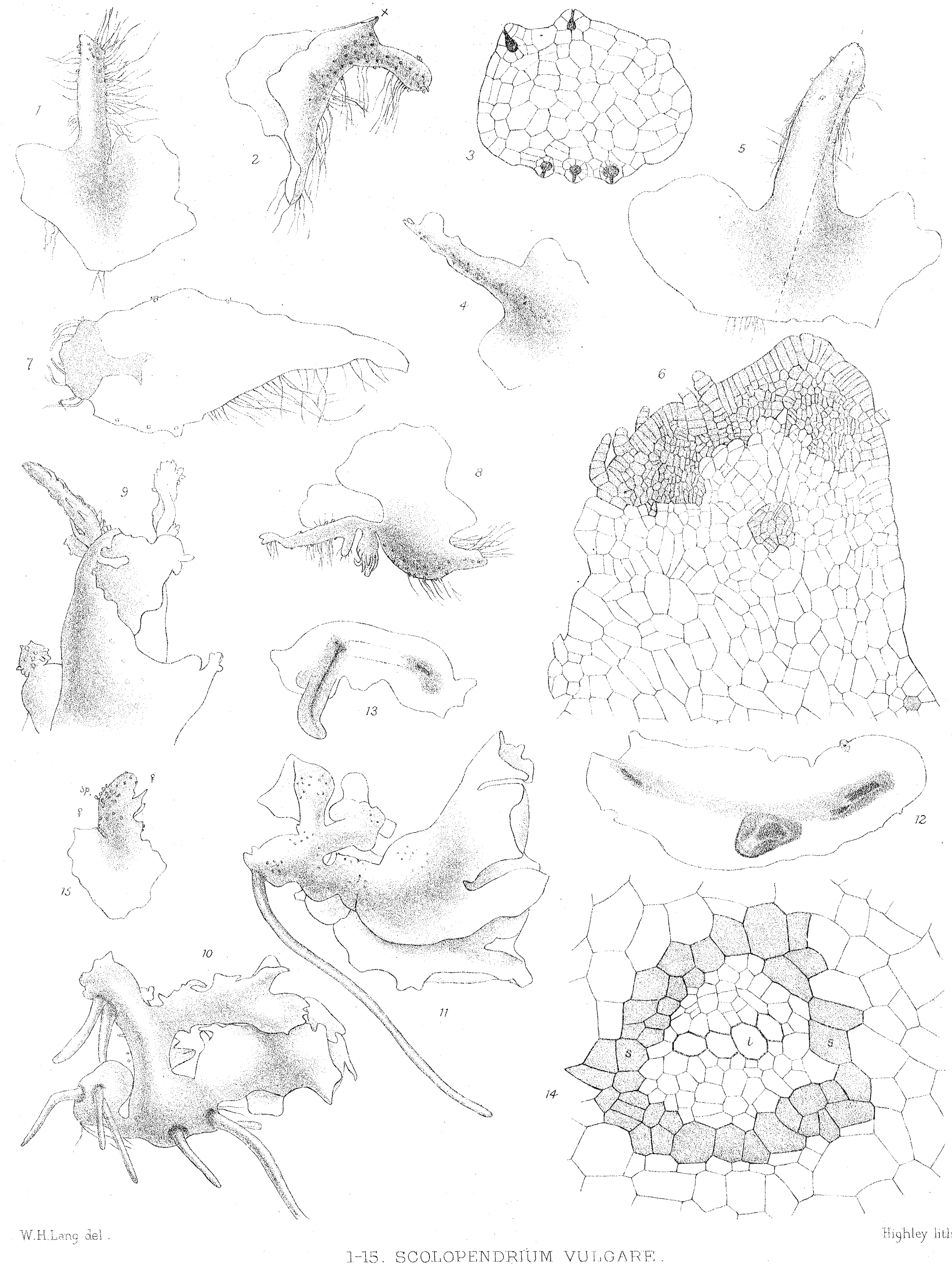
Fig. 79. Prothallus of *N. pseudo-mas* var. *polydactylum*, DADDS, in vertical section showing a bud developed from the under surface. (× 25.)

Fig. 80. Prothallus of same seen from the side. From the archegonial projection nearest to the apex a sporophyte arises.

Fig. 81. Somewhat similar prothallus seen from under surface.

Fig. 82. Similar prothallus, but only one archegonial projection has developed before the bud arose.

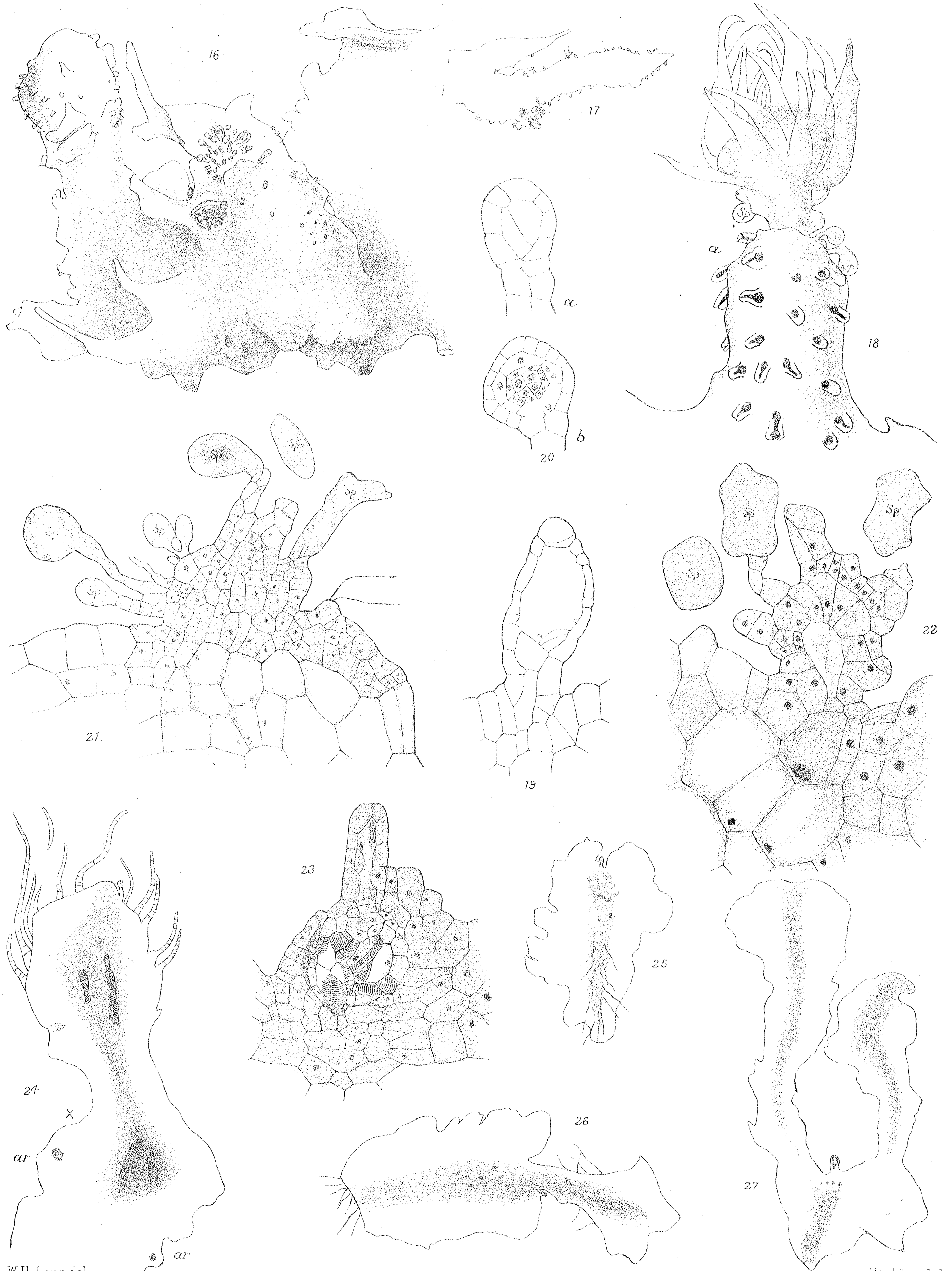
Fig. 83. Vertical section through such a prothallus as fig. 81, showing archegonial projections and bud. (× 25.)



W. H. Lang del.

Highley lith.

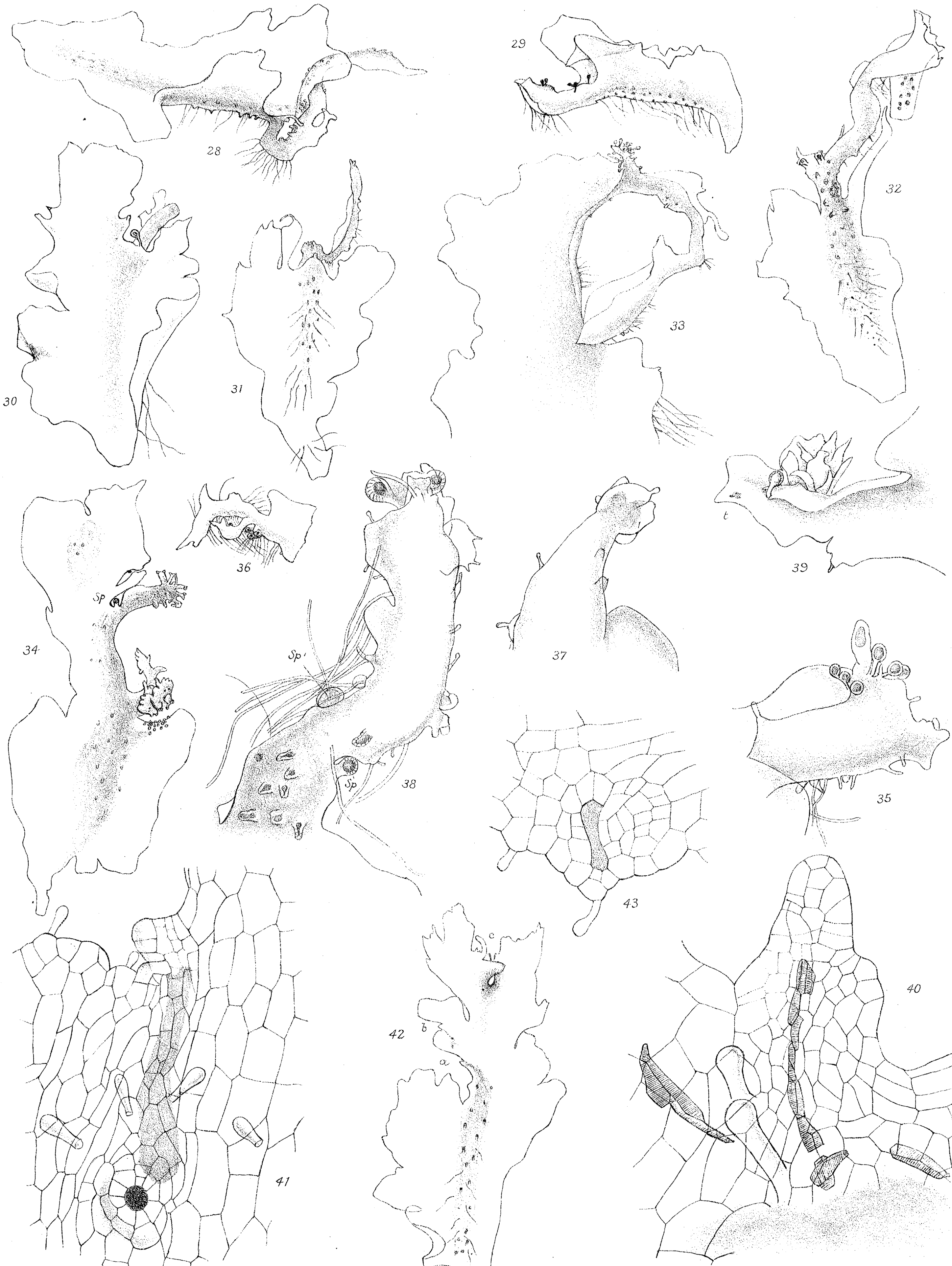
1-15. SCOLOPENDRIUM VULGARE.



W. H. Lang del.

Highley lith.

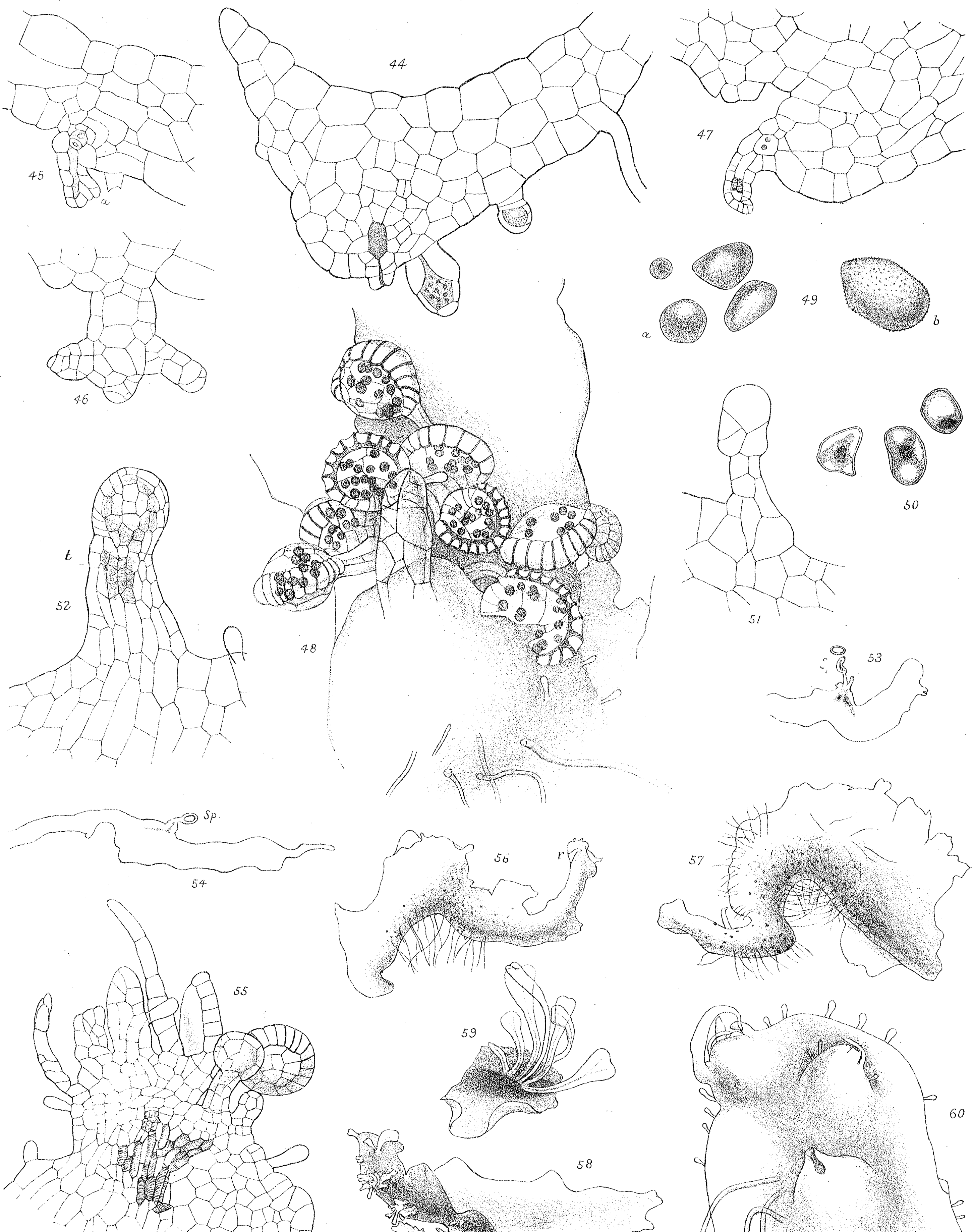
16–24. SCOLOPENDRIUM VULGARE. 25–27. NEPHRODIUM DILATATUM.



W.H.Lang del.

Highley lith.

28–43. NEPHRODIUM DILATATUM.



W. H. Lang del.

Highley lith.

44–55. NEPHRODIUM DILATATUM. 58–59. ASPIDIUM ACULEATUM.
60. ASPIDIUM ANGULARE.

W. H. Lang del.

Highley Lith.

61-65. ASPIDIUM ANGULARE. 67-68. ATHYRIUM NIPONICUM. 69. ASPIDIUM FRONDOSUM. 70-73. ATHYRIUM FILIX-FŒMINA
74-76. POLYPODIUM VULGARE. 77-88. NEPHRODIUM FILIX-MAS.

PLATE 7.

Scolopendrium vulgare.

Fig. 1. Prothallus from above, showing a cylindrical process developed from the apex.

Fig. 2. Prothallus from the side, showing a cylindrical process developed from the under surface. x = anterior margin.

Fig. 3. Transverse section of a thin cylindrical process. (× 70.)

Fig. 4. Cylindrical process re-assuming the prothalloid form.

Fig. 5. Prothallus with cylindrical process, the tip of which shows the first indication of developing into a sporophyte.

Fig. 6. Longitudinal median section of the tip of fig. 5, along the dotted line. The sporophytic tissue is shaded; the group of cells isolated in the figure was in connection with the main mass. (× 100.)

Fig. 7. Longitudinal section of a slightly older but similar bud; the sporophytic tissue is shaded. (× 25.)

Fig. 8. Prothallus of the variety *marginale*, showing a bud developed on a projection from the under surface.

Fig. 9. Terminal portion of a prothallus, on the under surface of which to the right is a prothalloid growth, and to the left a similar structure, which has continued as a simple leaf bearing ramenta. (× 25.)

Fig. 10. Prothallus from the branched cylindrical process of which ten roots arose; eight of these are visible.

Fig. 11. Prothallus of the variety *marginale*; a single root arises from the process on which archegonia are present.

Fig. 12. Longitudinal section of a cylindrical process, showing a young root still enclosed in the tissue. In the axial vascular strand, tracheides, the position of which is indicated by the dark shading, are present. (× 25.)

Fig. 13. Similar section of a part of the process in fig. 10, showing the insertion of an older root. (× 25.)

Fig. 14. Transverse section of the axial vascular strand in one of the branches of the process of fig. 10. T = tracheides. S = sheathing layer of cells. (× 300.)

Fig. 15. Prothallus with a thick flat process seen from above. *sp.* = sporangia. ♀ = archegonia.

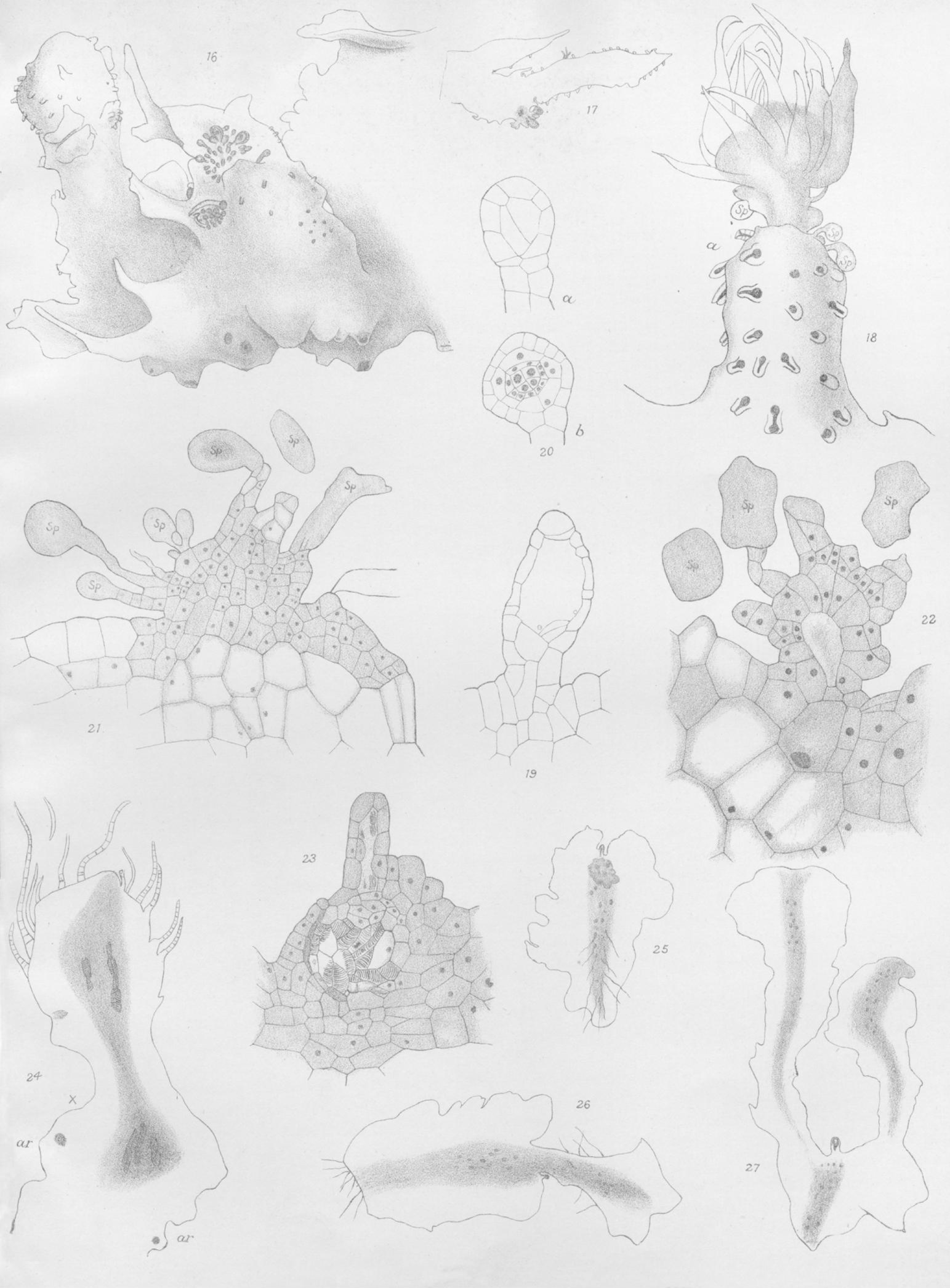


PLATE 8.

Scolopendrium vulgare.

Fig. 16. Prothallus with archegonial projections on the under surface, and on the massive cylindrical process two groups of sporangia; one of these groups is accompanied by two ramenta. (× 25.)

Fig. 17. Longitudinal section of a cylindrical process showing a group of well-developed sporangia on an archegonial projection in which tracheides, indicated by the dark shading, are present. (× 12.)

Fig. 18. Cylindrical process bearing sporangia on its tip along with a vegetative bud. *a.* = archegonia; *sp.* = sporangia. (× 25.)

Fig. 19. Longitudinal section of an imperfect sporangium. (× 170.)

Fig. 20. Normal sporangia in two stages of development: in *b*, the sporogenous group and the two layers of tapetum have become developed. (× 170.)

Fig. 21. Group of sporangia (sp.) from the prothallus in fig. 15, to show the contrast between the underlying tissue and that of the prothallus. In some of the cells of the sub-sporangial tissue two nuclei are present. (× 170.)

Fig. 22. Group of sporangia (sp.) on a projection, the structure of which indicates its relation to an archegonium. (× 600.)

Fig. 23. Group of tracheides developed beneath an archegonium neck. In some of these and in cells of the adjoining tissue two nuclei are present. (× 300).

Fig. 24. Longitudinal section of the process and bud in fig. 18. The vascular strand is shaded, the position of tracheides in it being indicated. *ar.* = archegonia; *x.* = level of attachment of the lowest sporangium. (× 25.)

Nephrodium dilatatum.

Fig. 25. Small prothallus with a well-developed middle lobe, viewed from the under surface. On the cushion are a number of archegonial projections.

Fig. 26. Prothallus with middle lobe bearing a rudimentary sporangium. Growth has taken place from the margin to one side of this.

Fig. 27. Prothallus, the middle lobe of which bears an imperfect sporangium of considerable size. Growth has taken place from the anterior margin on both sides of the apex.

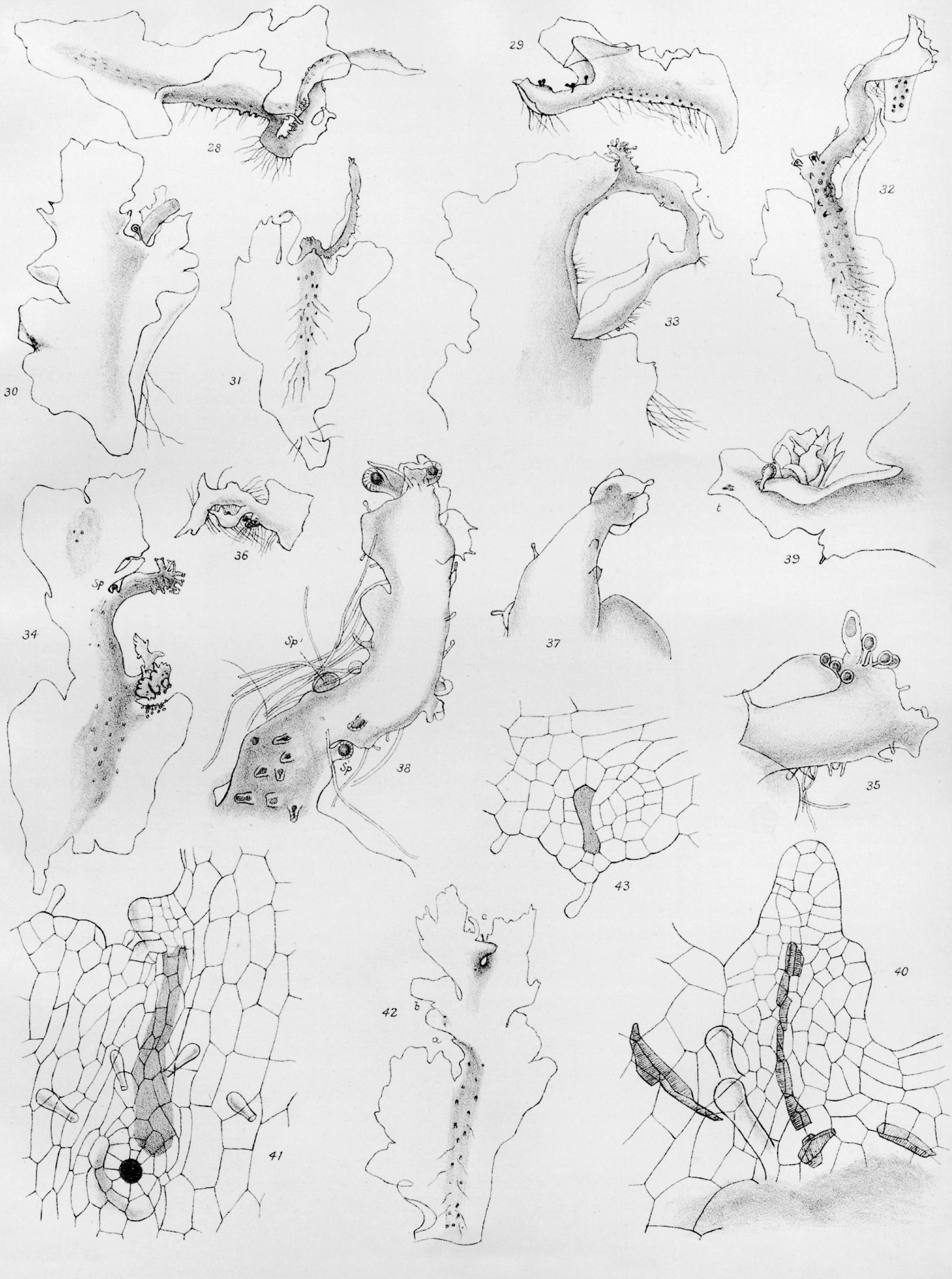


PLATE 9.

Nephrodium dilatatum.

Fig. 28. Prothallus from the side; the middle lobe bears a sporangium. On the under surface are small archegonial projections and behind the apex a cylindrical process which soon becomes flat and prothalloid.

Fig. 29. Prothallus from the side; a row of sporangia occupy the anterior margin and others are situated on the upper side of the cylindrical process.

Fig. 30. Prothallus from upper side; the middle lobe bears a perfect and almost mature sporangium: the process has retained its cylindrical form.

Fig. 31. Prothallus from above; the middle lobe bears an imperfect sporangium: the process soon becomes prothalloid.

Fig. 32. Prothallus from below; the apex continued directly as the cylindrical process: from behind the tip of this a similar process has arisen.

Fig. 33. Prothallus from the side; the middle lobe is represented by a group of sporangia situated on a flat branched structure.

Fig. 34. Prothallus from below; with two processes bearing abnormal archegonia. Sp. = rudimentary sporangium on middle lobe.

Fig. 35. Apex of prothallus on which a number of sporangia are situated. The one which corresponds to the apex of the middle lobe is more massive than the rest. The cylindrical process is still short. (× 25.)

Fig. 36. Cylindrical process from the under side of which a small branch of similar form arises; behind this a group of almost mature sporangia is situated among the rhizoids.

Fig. 37. Apex of a cylindrical process bearing ramenta; enclosed within these were young sporangia. (× 35.)

Fig. 38. Cylindrical process arising by the side of an imperfect sporangium (sp.); it bears a somewhat similar sporangium on the other side (sp.′), and on the tip are a number of sporangia associated with ramenta. (× 35.)

Fig. 39. Bud-like group of ramenta situated just behind the middle lobe which bears a sporangium. Tracheides were present in the thin continuation of the prothallus at *t*. (× 25.)

Fig. 40. Middle lobe from prothallus in fig. 25. (× 100.)

Fig. 41. Portion of the prothallus in fig. 42, including the middle lobe, *b*, and the strand of tracheides running from thence to an archegonium. (× 100.)

Fig. 42. Prothallus illustrating the nature of the cylindrical process, description in text. *a*, *b*, *c* = successively formed middle lobes; the last represented by a sporangium.

Fig. 43. Vertical section of an archegonial projection from a cylindrical process. (× 100.)

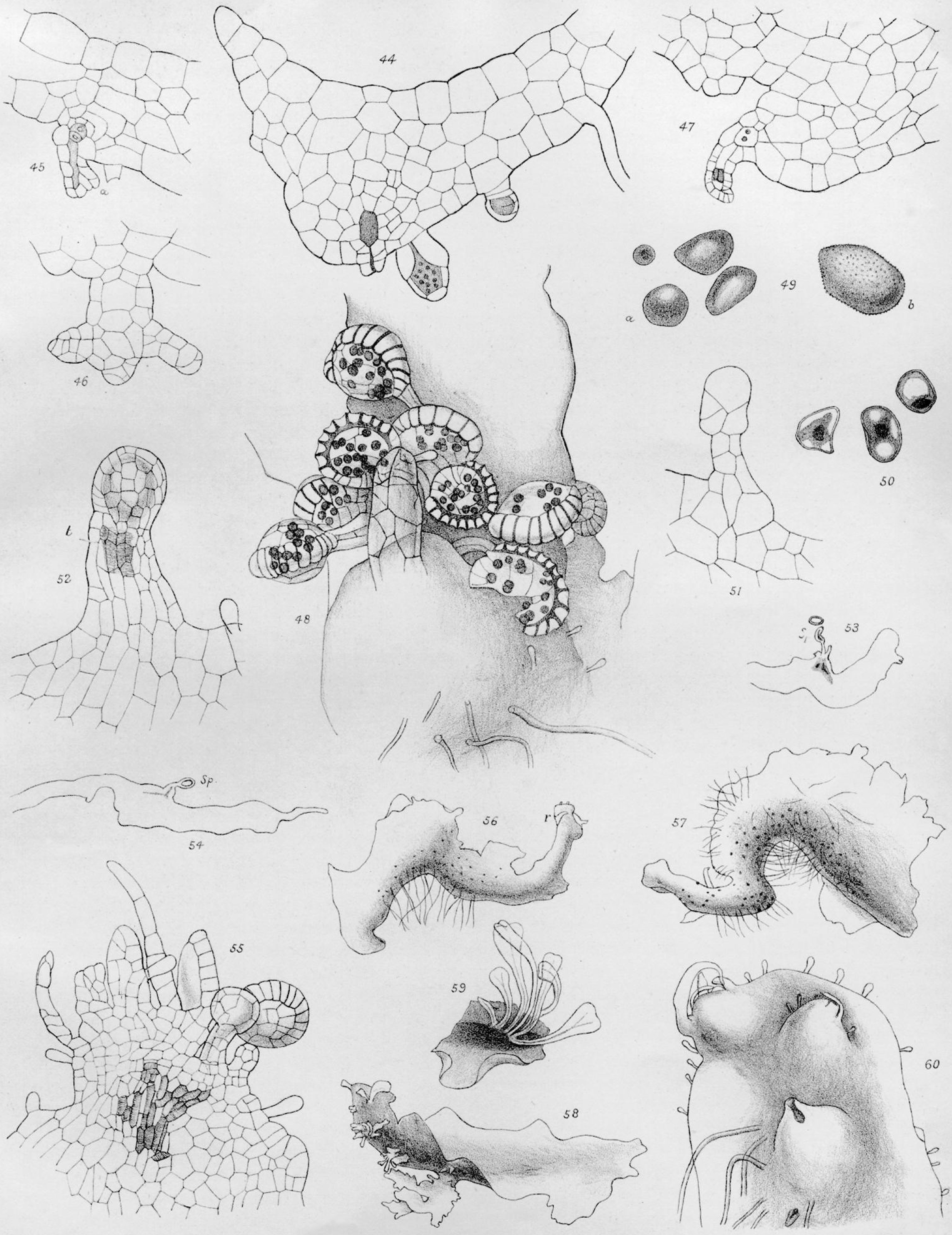


PLATE 10.

Nephrodium dilatatum.

Fig. 44. Vertical section of a rudimentary cylindrical process just behind the apex. (× 100.)

Fig. 45. An unopened archegonium, the cells of the neck of which have taken on further growth at *a*. (× 100.)

Fig. 46. Abnormal archegonium, the neck of which has grown on in three directions; seen from the outside. (× 170.)

Fig. 47. Vertical section of an archegonium, situated on a projection of the prothallus; in the canal of the neck two small tracheides have developed. (× 100.)

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Aspidium aculeatum.

Fig. 58. Old prothallus of a uniform brown colour, from the under side of which gametophytic budding has taken place in connection with archegonial projections. One of the growths resembles a cylindrical process at its origin.

Fig. 59. Similar prothallus bearing an apogamously-produced sporophyte; the six leaves of the latter are of similar simple form.

Aspidium angulare.

Fig. 60. Apical region of a prothallus seen from the under side; it bears an archegonial projection and two young buds, one of which arises from the margin. (× 25.)

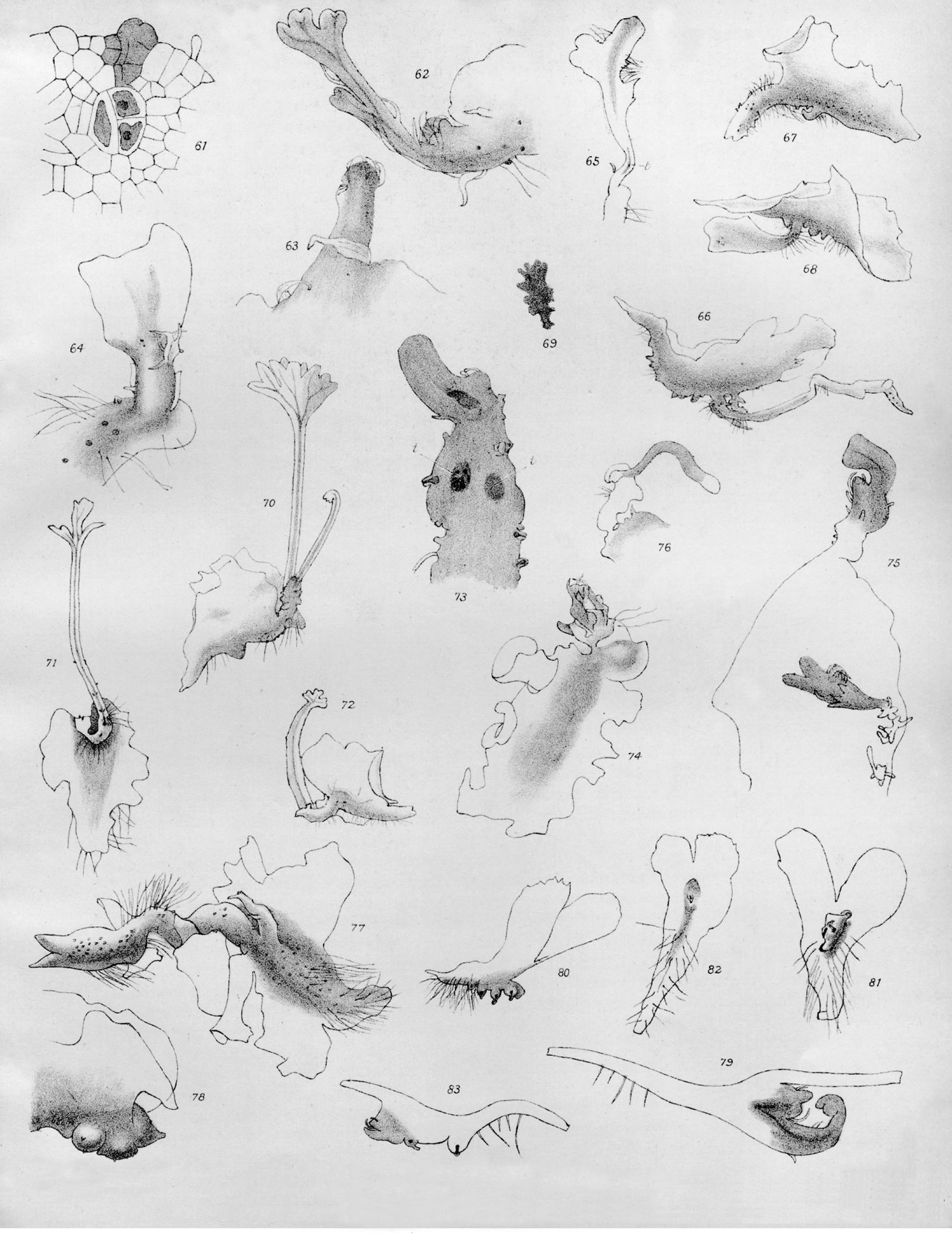

PLATE 11.

Aspidium angulare.

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Fig. 64. Growth bearing ramenta which arises in the position of a bud; its further growth is prothalloid. (× 25.)

Fig. 65. Growth with the characters of a leaf-stalk which has resumed the prothalloid form. t = tracheide.

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Fig. 77. Prothallus of *Nephrodium Filix-mas*, which continues as a thick almost cylindrical structure. The small cylindrical process which springs from the under surface bore a ramentum and contained tracheides.

Fig. 78. Anterior end of prothallus of the same variety; it bears archegonial projections. (× 25.)

Fig. 79. Prothallus of *N. pseudo-mas* var. *polydactylum*, DADDS, in vertical section showing a bud developed from the under surface. (× 25.)

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